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FIELD STUDIES ON THE EFFECTS OF AIRPLANE APPLICATIONS OF DDT ON FOREST INVERTEBRATES

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FIELD STUDIES ON THE EFFECTS OF AIRPLANE APPLICATIONS OF DDT ON FOREST INVERTEBRATES

INTRODUCTION

In 1944 and 1945 (Craighead & Brown 1945, 1946, Dowden *et al.* 1945) it was demonstrated that the aerial application of DDT to forests is an effective way of controlling defoliating insects, including important pests such as the spruce budworm (*Archips fumiferana* (Clem.)) and the gypsy moth (*Porthetria dispar* (L.)). The discovery that control could be obtained with a small amount of DDT per acre pointed to the feasibility of its use in airplanes against forest pests over large and inaccessible areas, where control had heretofore been impractical. The toxicity of DDT to most animals, however, raised the question of what damage it might do to the general faunas of the forests and streams. Studies were undertaken to follow the population fluctuations of forest invertebrates caused by experimental sprayings, and to obtain a measure of the tolerance of various species to DDT under natural conditions. The effects of treatments on parasites and predators were particularly studied, as was also the increase in the numbers of species resistant to the insecticide due in part to the reduction of their natural enemies. Information was also obtained on the duration of the residual effect of the poison. The present paper reports the studies on terrestrial forest invertebrates. Studies on aquatic invertebrates have been covered in another publication (Hoffmann *et al.* 1946). The effects of DDT on the vertebrates in the same areas have been reported on by the United States Fish and Wildlife Service (Cottam & Higgins 1946).

Five areas were selected for study, two of which were not treated and served as controls. Three of the areas were in gypsy moth-infested forests near Scranton, Pa., and two in moist bottomland forest on the Patuxent Research Refuge near Bowie, Md. The treated areas were sprayed by airplane with DDT in an oil solution. Area A (1,200 acres), near Scranton, was treated in the central part with about 4 pounds of DDT per acre and the remainder with 1 to 2 pounds. Area C (350 acres), also near Scranton, was sprayed with 1 pound of DDT per acre, and area D (117 acres) at Bowie was sprayed at the rate of 2 pounds of DDT per acre. Areas B and E were controls for and near areas A and D, respectively. Details regarding the nature of the forests, the formulation and dosage applied, and the effect of DDT on the faunas are given under the sections dealing with each area.

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METHODS OF STUDY

To obtain a reliable measure of differences in insect populations caused by the application of DDT, several population-sampling methods were used in the sprayed areas and control areas, shortly before the time of spraying and at intervals afterwards. Care was taken to select similar ecological habitats in both areas for comparison. For some species it was possible to obtain reliable quantitative data on abundance, whereas the abundance of others could only be estimated, with or without the aid of fragmentary quantitative data from the routine sampling work. Percent changes in population were computed for species where the data seemed most reliable. The percent reduction caused by DDT was calculated by the formula $(X\text{-}Y)100/X$, where X is the percent survival in the unsprayed area and Y is the percent survival in the sprayed area.

In an effort to measure the total effects of DDT on the more abundant terrestrial species, methods were employed to sample insects in a number of ecological habitats. Arboreal species were taken by tree jarring, and those arboreal forms killed by the spray were collected in large cloth-bottom trays placed on the ground to catch them as they fell. Flying insects were collected in light traps, fly traps, and box area traps, and on sticky trap boards. Ground species were collected in traps baited with rotten fish or molasses, and in modified Berlese funnels. Considerable data on flying and more sedentary species were obtained by sweep-net collections, by direct population counts in undisturbed habitats, and by general observations. Each method of study is described below, and information given on its operation, schedules, care of specimens, and the kinds of insects taken.

TREE JARRINGS

The tree-jarring method was used to make collections of tree-inhabiting insects that do not take to flight readily. Small understory trees (3 to 4 inches d.b.h.), the crowns of which did not touch adjacent trees, were selected for sampling. Two large cloths, each 6 by 9 feet, were spread beneath a tree so that insects falling would drop on them. The tree was jarred by hitting the trunk 10 hard blows with an ax. After the tree was jarred, the edges of each cloth were pulled together in an upward motion so as to concentrate the insects and debris. The insects were then picked up with forceps or a suction aspirator and placed in vials containing 70% alcohol.

A number of white oak and red maple trees, species that predominated in areas A and B, were jarred once before spraying was started and again at approximately 12 days, 1 month, 2 months, and 1 year afterwards. Though care was taken to place the sheets beneath the tree canopy, to strike similar blows with the ax, and to avoid sampling when there was a breeze, the collections ranged from no specimens to several dozen. Species collected in numbers included lepidopterous larvae, springtails, ants, spiders, and mites (table 1).

COLLECTION TRAYS

The collection trays consisted of a 3 by 3-foot wooden frame of 1-inch stock with heavy white muslin tacked on the back. To keep dying insects from crawling out, a 3-inch collar of heavy building paper was tacked around the wooden frame. The trays were placed on the ground, usually beneath trees, at intervals of 25 yards. The invertebrates found in the trays were periodically removed with forceps or with a suction aspirator and transferred to vials containing alcohol.

In area A, 43 trays were set out along a trail in a valley extending from one boundary to the middle of the plot. Six additional trays were similarly spaced below the boundary in the area that was unsprayed, but nevertheless covered by spray drift. Only 10 trays were used in area B; so the numbers in collections there were multiplied by 5 to give an approximate comparison with those made in the area receiving spray. Collections were made daily from May 16 to June 9 and then on alternate days through August 21. Over 370 species or groups were found in the tray collections. Of 4,457 specimens collected in area A, Diptera made up 41%, Lepidoptera 17%, Homoptera 16%, Hymenoptera 12%, and Coleoptera 9% (table 2). Ants carried off many specimens from the trays, so the collections from them can be used in a general and comparative way, but not as quantitative area sampling.

In area C, 21 trays were placed beneath trees. Collections were made daily for about a week after the spraying and then usually on every other day.

In areas D and E, 12 trays each were placed under trees. Daily collections were made in both areas from June 1 to June 16, and thereafter every second or third day through July 16.

LIGHT TRAPS

The light trap used was a modification of the portable light designed by Burks *et al.* (1938). (Fig. 1.) The light source was an argon-mercury discharge tube wound in a flat coil of 2 turns, 5½ inches across. The light emitted was blue, rather dim but constant. In the locations used the light could be seen for about 150 yards through the woods. Power was supplied by a standard automobile storage battery stepped up with a Ford model-T spark coil. The battery operated between 50 and 60 hours without recharging. Immediately below the light a galvanized-iron funnel, 18 inches across the top, was used

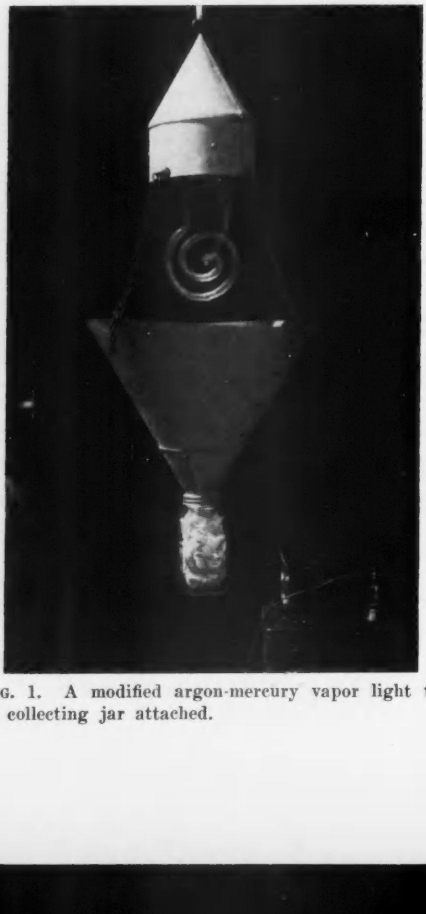

FIG. 1. A modified argon-mercury vapor light trap with collecting jar attached.

TABLE 1. Total numbers of selected invertebrates taken by jarring trees in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Invertebrates	White Oak[1]										Red Maple[2]										Population 3 months after treatment
	1945								1946[3]		1945								1946[3]		
	May 9		June 12		June 30		Aug. 28		May 24		May 14		June 12		June 30		Aug. 28		May 24		
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
Collembola	0	0	3	26	85	8	104	5	0	0	0	0	0	5	5	2	140	3	..	..	Increased
Heteroptera (nymphs):																					
Phytocoris sp.	7	1	0	6	0	3	0	3	0	0	6	4	0	2	0	1	0	0	0	0	Eliminated
Cicadellids	6	0	0	1	0	0	0	0	0	0	5	6	0	3	0	1	0	1	0	1	Eliminated
Coleoptera:																					
Pinacodera platicollis	1	0	0	2	0	0	1	13	0	0	0	0	0	0	0	1	1	3	0	1	Survived
Coccinellid larvae	6	1	0	0	0	0	2	0	5	0	2	0	0	0	0	0	1	0	0	1	....
Lepidoptera (larvae):																					
Phigalia titea	0	0	0	2	0	0	0	0	0	0	7	10	0	0	0	0	0	0	0	0	Eliminated
Other geometrids	0	0	0	5	0	0	0	0	1	1	121	42	0	4	0	1	0	0	3	1	Eliminated
Nadata gibbosa	0	0	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0	2	0	0	....
Porthetria dispar	33	1	0	1	0	0	0	0	0	0	49	0	0	0	0	0	0	0	0	0	Eliminated
Cosmia canescens?	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	Eliminated
Other	8	1	0	12	0	0	1	15	3	5	32	12	0	4	0	1	0	3	1	5	Greatly reduced
Diptera:																					
Syrphid larvae	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	3	0	0	0	....
Hymenoptera:																					
Camponotus fallax	5	0	0	4	0	3	0	0	0	0	2	0	0	4	0	20	0	1	..	..	....
Formica fusca subsericea	1	0	0	1	1	23	0	1	0	0	7	5	0	5	0	6	0	0	..	..	....
Lasius niger	0	3	0	2	2	50	0	5	0	0	2	3	0	6	5	128	0	0	..	..	....
Acarina:																					
Mites	12	2	308	102	10	6	179	1	0	0	29	14	7	42	0	1	274	34	..	..	Increased
Araneae:																					
Theridion alabamense	0	2	0	6	1	3	4	7	2	1	0	0	0	0	1	0	0	2	0	2	Not reduced
Theridion murarium	10	4	0	8	0	0	2	6	0	0	11	7	0	2	0	2	0	2	0	2	Greatly reduced
Theridion kentuckyense	7	3	0	1	0	0	0	3	0	2	3	0	0	0	0	0	0	0	0	1	Eliminated
Coriarachne versicolor	1	6	3	4	1	4	0	3	2	1	0	0	0	0	0	0	1	0	0	0	Not reduced
Philodromus pernix	8	10	0	7	0	0	4	5	1	7	1	0	0	1	1	0	2	1	1	0	Moderately "
Clubiona spp.	0	0	0	4	0	13	1	9	1	4	0	0	0	1	1	3	1	7	0	2	Survived
Metaphidippus protervus	1	0	0	2	0	0	0	11	0	4	3	8	0	2	0	0	0	10	0	2	Greatly reduced

[1]On June 12, 4 white oak trees in area A and 3 in B were jarred; on all other dates 6 trees were jarred in each area.
[2]On June 12, 3 red maple trees were jarred in areas A and B; on all other dates 7 trees were jarred in each area.
[3]Species of Collembola, ants, and mites were numerous in 1946 but were not collected.

to collect the insects and to direct them into a 1-quart glass jar. A paper-wrapped cotton pad soaked with carbon tetrachloride was put in the bottom of the jar, which was filled loosely with strips of paper toweling. The chemical fumes remained strong for the period the light was in operation, and moths were killed with a minimum of fluttering. Specimens collected were sorted to orders, counted, layered between Cellu-cotton in cardboard boxes, and stored for later determination.

The light trap was hung either from a horizontal tree branch or from a board nailed between trees, with the light unit about 6 feet from the ground, and was wired to the ground to prevent swinging in the wind. A wooden frame above the trap supported strips of heavy building paper to keep out rain. Brush was cleared away for a 10-foot radius.

One trap was placed in area A and another in a similar habitat in area B. Runs of 3 hours nightly were made beginning May 12, 1945, starting shortly after dark at 9 or 9:30 p.m. and continuing until midnight or 12:30 a.m. Beginning July 1, runs were made 2 nights a week until August 21. On nights of continuous rain or low temperatures collections were not taken. Runs were also made May 22-24, 1946. Temperature was recorded at the beginning and close of each run, and notes were taken on the weather conditions.

Another light trap of the same design was used in area D and one in area E, where runs of 2 hours nightly were made from May 30 to June 17 and at less frequent intervals through July 12.

The kinds of insects caught in the light traps are shown in tables 3, 4, 11, and 12.

FLY TRAPS

The fly trap used was of a standard pattern (Bishopp 1937), consisting of an upright cylinder of 16-mesh wire screening 2 feet high and 18 inches in diameter, tacked to a wooden frame. Short legs kept the base of the cylinder about 1 inch above the platform, so that flies would enter through this gap to the bait pan and then fly up into a large screen funnel extending upwards into the cylinder. The top of the trap contained a door through which the trap was emptied. A cellulose acetate window in this door let in light so that the flies would climb the funnel, and kept rain from the specimens and

TABLE 2. Total numbers of insects collected in trays in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Order	Area	MAY			JUNE				JULY				AUGUST			Percent of total catch
		16-22	23-29	30-5	6-12	13-19	20-26	27-3	4-10	11-17	18-24	25-31	1-7	8-14	15-21	
Collembola	A	1	2	0	3	1	0	5	5	5	0	0	1	1	0	1
	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neuroptera	A	0	13	1	3	2	1	3	0	0	0	0	0	0	0	1
	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plecoptera	A	0	11	5	7	0	0	0	0	0	0	0	0	0	0	1
	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heteroptera	A	2	52	8	4	1	0	0	0	0	0	0	1	1	0	2
	B	0	0	0	0	0	0	5	0	0	0	5	0	5	0	1
Homoptera	A	11	296	145	36	28	34	67	17	34	5	4	12	28	18	16
	B	0	0	0	0	0	0	0	0	0	0	20	5	5	0	2
Coleoptera	A	20	135	79	87	33	3	14	6	11	5	5	7	9	5	9
	B	25	15	25	25	10	0	5	0	0	5	5	5	5	0	7
Lepidoptera	A	21	509	77	46	29	12	13	10	11	7	7	5	6	2	17
	B	20	15	35	30	0	15	5	5	5	0	5	10	5	0	8
Diptera	A	67	694	173	286	64	66	118	63	57	63	106	60	12	6	41
	B	60	0	15	5	0	30	15	20	20	165	585	415	85	15	76
Hymenoptera	A	24	196	52	55	36	9	36	18	38	5	11	14	34	19	12
	B	10	0	0	5	5	5	20	0	10	15	15	20	20	10	7
Other Orders	A	0	14	2	4	3	0	0	1	0	0	0	0	3	0	1
	B	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Totals[1]	A	146	1922	542	531	197	125	256	120	156	85	133	100	94	50	
	B	115	30	75	70	15	50	50	25	35	185	635	455	125	25	
Percent of total catch	A	3	43	12	12	4	3	6	3	4	2	3	2	2	1	
	B	6	1	4	4	1	3	3	1	2	10	33	24	7	1	

[1]Total numbers of insects collected in area A, 4,457; in area B, 1,890.

bait. A trap platform was nailed to a tree about 5 feet from the ground. The bait used was stale beer, which was placed in a low circular pan 12 inches across, resting on a platform immediately below the funnel. The bait in both the sprayed and control areas was from the same stock, and was changed at the same times. Traps were covered during the spray applications to prevent contamination.

When a trap was to be emptied, a sheet of wet paper was placed underneath it on the ground, two cloth sheets were folded to envelop it, and the edges tucked around its base. The trap was then momentarily tilted and a small quantity of calcium cyanide was placed on the sheet of paper. After about 10 minutes the flies were either killed or stupified, whereupon they were concentrated on one sheet and emptied into a jar containing a cotton plug saturated with carbon tetrachloride.

The large size of most catches made tabulation of all specimens impractical. Specimens other than Diptera were removed, and their numbers recorded. The number of remaining specimens was then estimated, a random sample of 100 specimens was taken for identification, and the remainder were discarded. If the catch was small, all specimens were identified and the sampling method was not used.

One fly trap was placed in each of areas A and B. These traps were run and emptied daily from May 12 to June 13, run on alternate days from June 14 to July 1, and then run for 2-day intervals twice a week through August 25. During this time about 6,000 calypterate Diptera were taken in the sprayed area and about 33,000 in the control area. These Diptera represented about 50 species.

One trap was used in each of areas D and E, where they were run and emptied daily from May 29 to June 17, and once or twice a week from June 19 to July 26. During the 8-day period before the spray application, the trap in the control area (E) took about twice as many specimens as did the trap in the area to be sprayed (D). Approximately 4,100 calypterates were taken in area D and about 9,300 in area E. About 40 species were represented.

Calypterate flies were the dominant forms collected, and those taken in greatest numbers are considered in table 5. Other Diptera taken in fairly large num-

TABLE 3. Average numbers of insects per collection taken in light traps in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Order	MAY 16-31 (10)[1]		JUNE 1-15 (5)		JUNE 16-30 (5)		JULY 1-15 (4)		JULY 16-31 (3)		AUGUST 1-15 (4)		AUGUST 16-31 (2)		Population 2 weeks after treatment
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
Orthoptera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	......
Neuroptera	0	1	0	0	0	5	1	1	2	0	2	1	1	0	......
Heteroptera	0	0	0	0	0	0	0	0	0	1	0	0	0	0	......
Homoptera	1	0	0	0	1	39	0	0	0	1	2	1	3	4	......
Coleoptera	3	2	1	14	4	24	3	9	23	27	3	26	2	5	Greatly reduced?
Trichoptera	0	0	0	1	2	7	1	2	1	6	1	0	0	1	......
Lepidoptera	4	13	38	146	62	466	117	467	378	539	193	328	67	71	Moderately reduced
Diptera	28	43	32	46	76	158	163	83	688	612	70	22	18	4	Not reduced
Hymenoptera	0	1	0	2	6	3	3	1	8	1	2	2	1	0	......

[1] Figures in parentheses represent numbers of collections made.

bers were Fungivoridae, Sylvicolidae, Drosophilidae, Lauxaniidae, and Syrphidae. There were also a considerable number of Lepidoptera, and some Vespidae and Trichoptera.

STICKY TRAP BOARDS

Sticky trap boards were originally designed for pear psylla research and were developed by Kaloostian and Yeoman (1944). The boards used in this study were of thin wood and heavy cardboard, 4 by 8 inches, painted bright orange-yellow, and covered with a transparent, waterproof substance which remained sticky for a considerable period. The traps were hung from branches by short pieces of wire.

In each of areas A and B, six sticky trap boards were hung at a height of about 7 feet at 25-yard intervals. Comparable habitats were selected in the two areas and the individual sites were marked and used for successive sets of boards throughout the summer. Two sets were exposed before treatment, 1 for 5 and 1 for 3 days. Runs resumed after the DDT treatment were usually of 6 days' duration, and were continuous from June 2 to August 26.

For areas D and E ten sticky boards were hung in each at an average height of 3 feet and at intervals of 25 yards. One set was exposed for 3 days in each area before the spray application on June 5 and two similar sets for 3 days immediately after the spray application. After June 8 additional sets were exposed for 1 week each in both areas through July 9.

The sticky trap boards were transported and stored in wooden boxes that held the boards, about 30 to a box, much as slide boxes hold slides. Separation of the boards in the boxes was obtained by a row of flatheaded nails near the top and another row near the bottom of each side, the spacing between the nail heads being slightly greater than the thickness of the boards. Each box had a cover and a strap for convenient carrying. A wooden holder was made to facilitate examination of the boards. Small nails were driven at scattered points to extend upwards through a light board, which was slightly larger than the trap board, and a narrow board was nailed along each side. The sticky trap board when placed on the points of nails in the holder could be moved back and forth under a binocular microscope for counting and identifying the specimens without danger of the operator touching the adhesive.

TABLE 4. Average numbers of selected Macrolepidoptera per collection taken in light traps in areas A and B before and after Area A was sprayed with DDT. Spraying begun on May 20, 1945.

Species	MAY 12-31 (13)[1]		JUNE 1-30 (11)		JULY 1-31 (7)		AUGUST 1-31 (6)		Population 1 month after treatment
	A	B	A	B	A	B	A	B	
Phalaenidae:									
Agrotis ypsilon	0.0	0.2	0.3	1.9	0.0	0.1	0.0	0.0	Not reduced
Amanthes c-nigrum	0.2	0.3	8.6	12.4	0.3	0.0	0.0	0.0	Not reduced
Polia latex	0.1	0.4	0.5	1.0	0.0	0.0	0.0	0.0	Not reduced
Orthodes cynica	0.0	0.0	2.2	6.3	0.3	0.1	0.0	0.0	......
Pseudorthodes vecors	0.0	0.0	0.2	1.5	0.1	0.0	0.0	0.0	......
Crocigrapha normani	0.4	1.4	0.0	0.0	1.6	0.0	0.2	0.0	......
Cirphis unipuncta	0.0	0.1	0.4	1.2	0.0	0.1	0.0	0.0	Not reduced
Phlogophora iris	0.0	0.0	0.8	3.1	0.0	0.0	0.0	0.0	......
Elaphria festivoides	0.3	0.5	2.4	11.8	0.0	0.0	0.0	0.0	Moderately reduced
Cosmia canescens	0.0	0.0	0.0	0.0	1.3	0.0	0.0	1.2	......
Zale unilineata	0.6	1.8	0.1	0.0	0.0	0.0	0.0	0.0	......
Epizeuxis aemula	0.0	0.0	0.4	9.8	10.0	28.4	9.5	10.8	Not reduced
Epizeuxis rotundalis	0.0	0.0	0.0	20.5	21.4	18.3	47.0	20.2	Not reduced
Zanclognatha lituralis	0.0	0.0	0.0	1.4	1.3	3.7	0.0	0.0	Not reduced
Zanclognatha laevigata	0.0	0.0	0.0	0.4	1.1	0.7	0.0	0.0	Not reduced
Zanclognatha pedipilalis	0.1	0.2	0.5	3.4	0.0	1.1	0.0	1.5	Slightly reduced
Zanclognatha ochreipennis	0.0	0.0	0.0	0.3	1.3	1.6	0.7	5.0	Not reduced
Notodontidae:									
Nadata gibbosa	0.0	0.1	0.2	0.3	0.1	0.6	0.0	0.0	Not reduced
Geometridae:									
Physostegania pustularia	0.0	0.0	0.0	0.4	2.1	5.6	0.0	12.8	Not reduced
Pero honestarius	0.2	0.5	0.0	0.4	0.1	0.0	0.5	2.3	Slightly reduced
Abbottana clemataria	0.2	0.7	0.0	0.2	0.1	0.0	0.0	0.3	Slightly reduced
Other Macrolepidoptera	1.4	3.5	2.5	13.3	3.1	7.7	0.7	3.3	Moderately reduced
Totals	3.5	9.7	19.1	89.6	44.2	68.0	58.6	57.4	Moderately reduced

[1] Figures in parentheses represent numbers of collections made.

The insects caught on one-third of the surface of each sticky trap board exposed in areas A and B in 1945 were tabulated, whereas all the insects on the entire surface of the boards were considered in the 1946 collections and in all collections from areas D and E. For areas D and E over 52,000 specimens were tabulated. The types of insects captured by this method are indicated in tables 6 and 14.

TABLE 5. Average daily catch and percent reduction of calypterate flies taken in fly traps in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Species	May 14-31		June-July		Average percent reduction
	A	B	A	B	
Calliphora spp.	42	146	19	87	25
Phormia regina	74	219	8	52	54
Pyrellia cyanicolor	30	78	0.1	38	99
Muscina assimilis	4	42	6	85	26
Hydrotaea dentipes	8	57	3	23	None
Hylemya cilicrura	22	17	1	109	99
Fannia manicata	0.5	5	4	35	None
Fannia canicularis	2	21	0.05	9	94
All calypteratae	225	695	49	552	72

BOX AREA TRAPS

Each box area trap consisted of a large plywood box, 4 feet square at the base and 3 feet high, open at the bottom, and on 1 side near the top a 15-inch circular window covered by a cellulose acetate funnel opening outward into a one-half pint jar (Fig. 2). The funnel was 15 inches in diameter at the base, and tapered to about 2 inches at the top. It was 9 inches deep and obliquely truncate, so that the upper surface was horizontal and the lower strongly sloping. At the apex of the funnel was fastened a metal bottle top, the middle cut out to fit the opening of the funnel, so that a glass jar could be screwed on. A small amount of 70% alcohol was kept in the jar. The boxes were painted black within, and were made so that all edges were light proof. The sides were fastened together with bolts and wing nuts for assembly or knock-down in the field.

Two box area traps were used in area A, 1 in a moist site and 1 in a drier site, and 2 in similar situations in area B. In the study areas the vegetation of the forest floor was uneven. To standardize collections, 6 plots, approximately similar in vegetation, were staked out at each location. The boxes were rotated on these areas, and each collection was largely of positively phototropic insects taken during a 24-hour period. In areas A and B collections were

TABLE 6. Total numbers and percent reduction of insects collected on sticky trap boards in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Order or Family	1945										Percent reduction due to DDT after about 6 weeks	1946	
	May 9-17		June 2-15		June 21-July 9		July 15-August 2		August 8-26			May 22-28	
	A	B	A	B	A	B	A	B	A	B		A	B
Thysanoptera	378	243	6	16	6	8	7	6	0	5	..	20	32
Heteroptera	1	1	9	0	2	3	0	2	2	4	..	0	11
Aleyrodidae	100	76	12	39	6	22	93	242	16	49	79	1,360	568
Aphiidae	4	6	31	22	70	29	79	24	158	35	..	18	37
Cercopidae	1	0	0	2	37	50	16	13	9	9	..	0	0
Cicadellidae	94	70	1	13	9	80	6	98	4	27	92	40	171
Membracidae	1	0	0	0	1	80	0	2	0	3	..	0	0
Cantharidae	0	3	2	10	4	29	4	15	1	1	..	0	5
Staphylinidae	1	1	1	11	2	2	0	14	1	5	..	2	8
Chrysomelidae	6	9	1	13	2	16	0	20	0	2	81	3	11
Lepidoptera	0	0	2	41	2	14	2	19	2	1	..	0	5
Lycoriidae	229	281	1	37	42	162	9	12	12	14	69	273	86
Fungivoridae	7	11	2	8	31	45	19	79	21	20	..	11	16
Tendipedidae	446	523	11	54	8	28	2	4	5	14	60	389	858
Itonididae	7	6	14	23	137	57	238	105	88	27	..	52	89
Empididae	26	53	2	17	1	7	0	3	0	2	..	44	57
Dolichopodidae	1	2	2	5	3	10	2	19	2	5	..	1	1
Phoridae	25	44	5	50	22	493	35	339	20	57	92	29	100
Lauxaniidae	17	68	4	40	2	18	3	35	1	11	54	3	49
Braconidae	11	6	4	10	9	28	7	9	4	9	82	4	2
Ichneumonidae	18	12	5	23	4	29	7	20	5	13	91	8	6
Diapriidae	6	8	0	11	6	36	2	12	0	2	78	2	1
Calliceratidae	10	7	9	35	17	98	7	28	7	8	88	5	4
Platygasteridae	78	33	4	19	7	29	2	10	8	6	90	78	86
Cynipidae	23	12	2	10	28	48	8	3	0	0	69	387	76
Chalcidoidea	132	99	2	28	37	105	14	27	9	9	74	201	110
Other insects	104	70	9	78	13	76	0	130	18	22	..	349	219
Totals	1,726	1,644	141	615	508	1,602	562	1,290	393	360	70	3,279	2,608

made almost daily from May 14 through June 12, after which runs of 4 consecutive days each were made beginning on the following dates: June 28, July 11, and August 20. The same traps were used in a similar manner in areas D and E. There the vegetation was more uniform and the boxes were moved to a new location each day. Consecutive daily runs were made from June 16 to 21.

FIG. 2. Box area trap with collecting jar screwed to funnel.

Specimens collected were transferred to vials of alcohol for storage and later determination. The most abundant species taken in areas A and B are given in table 7.

SWEEPING

The nets used for sweeping were constructed of a strong unbleached muslin bag attached to a heavy wire ring, 12 inches in diameter. Ordinarily two men swept for ½ or 1 hour in a selected habitat in the sprayed area, and soon after on the same day in a similar site in the control area. Different kinds of plants were swept within a radius of 50 yards of a selected point, and these provided specimens of many insects and spiders.

Two sweep collections were made in areas A and B shortly before A was sprayed, and others were made about biweekly for the next 3 months. Area D was sampled a week before the spray application, and both D and E were sampled at weekly intervals for 1 month afterwards.

Several methods were used to separate the insects from the vegetable debris swept with them into the

TABLE 7. Total numbers of insects collected in box area traps in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Species	Area	May 14-18	May 24-31	June 2-7	June 8-12	June 29-July 2	July 12-15	Aug. 21-24	Population after treatment	
		(10)[1]	(10)	(10)	(10)	(8)	(8)	(8)	2 weeks	3 months
Thysanoptera:										
Thripidae										
Frankliniella tritici	A	39	0	0	0	0	0	0	......	......
	B	91	10	0	10	0	0	0		
Diptera:										
Lycoriidae										
Lycoria spp.	A	150	361	2	0	7	84	10	Greatly reduced	No reduction?
	B	513	391	5	149	297	66	6		
Sphaeroceratidae										
Leptocera spp.	A	5	0	0	1	1	6	14	Moderately reduced?	No reduction
	B	19	11	0	4	17	3	15		
Phoridae										
Borophaga femorata	A	0	1	0	0	53	15	33	......	No reduction
	B	2	0	0	0	139	15	39		
Megaselia spp.	A	45	41	15	7	36	115	403	Greatly reduced	No reduction
	B	75	53	3	127	93	120	384		
Drosophilidae										
Chymomyza amoena	A	45	6	0	4	22	10	1	Moderately reduced?	......
	B	29	7	1	9	12	1	0		
Drosophila inversa	A	39	8	0	12	42	16	9	No reduction	No reduction
	B	36	20	0	9	39	8	15		
Hymenoptera:										
Diapriidae										
Xenotoma sp.	A	6	1	1	0	8	18	4	Greatly reduced?	No reduction?
	B	12	6	1	6	12	21	3		
Platygasteridae										
Leptacis sp.	A	10	0	0	0	3	0	14	Greatly reduced?	Moderately reduced?
	B	0	3	0	1	11	8	31		
Totals	A	339	418	18	24	172	264	488		
	B	777	501	10	315	620	242	493		

[1]Figures in parentheses represent the numbers of samples of the most abundant insects collected.

TABLE 8. Total numbers of ground-inhabiting Coleoptera attracted to ground traps baited with fish in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Species	2 weeks before spray		AFTER SPRAY— 1 week		4 weeks		12 weeks		1 year after spray		Population 1 week after treatment
	A	B	A	B	A	B	A	B	A	B	
Silphidae:											
Catops simplex	6	0	1	22	1	16	1	12	0	0	Greatly reduced
Nicrophorus orbicollis	7	8	0	20	1	18	0	0	1	8	Eliminated
Nicrophorus defodiens	6	18	0	32	0	2	2	10	0	6	Eliminated
Nicrophorus sayi	7	12	0	4	0	2	0	0	1	2	Eliminated
Nicrophorus tomentosus	0	0	0	0	0	0	23	42	0	0	......
Prionochaeta opaca	1	0	2	4	1	2	0	0	0	0	......
Silpha americana	8	12	0	0	13	4	0	0	1	6	......
Silpha noveboracensis	0	34	0	0	65	22	0	0	0	0	......
Scarabaeidae:											
Dialytella dialytoides	0	0	3	14	0	2	0	0	0	0	......
Geotrupes balyi	1	0	1	16	46	60	41	32	0	0	......
Onthophagus hecate	10	4	0	4	4	2	0	0	5	2	Eliminated?
Carabidae:											
Carabus limbatus	21	16	0	4	0	4	0	2	1	10	Eliminated
Euferonia lachrymosa	0	0	0	0	0	0	7	2	0	0	......
Pterostichus adoxus	0	0	1	2	5	0	24	10	4	2	......
Pterostichus mutus	7	0	1	4	1	0	6	0	13	11	......
Staphylinidae:											
Ontholestes cingulatus	4	10	7	0	1	0	0	0	1	3	Not affected
Philonthus cyanipennis	0	0	4	2	5	2	1	0	9	12	Not affected
Staphylinus viridanus	0	0	0	0	5	4	4	0	0	3	......
Tachinus fimbriatus	0	0	0	0	0	0	6	0	0	0	......
Tachinus spp.	12	58	0	12	18	4	5	2	2	4	......
Histeridae:											
Hister spp.	0	2	4	2	6	4	2	0	5	1	Not affected
Other Coleoptera	12	4	10	12	12	8	12	12	1	2	......
Totals	102	178	34	154	184	156	134	124	44	72	62 percent reduction

nets. On warm days, after a considerable quantity of insects and debris had been swept, the material was put through a small door into a separator box. This was a wooden box of tight construction, with a door for introducing sweepings at one end near the top, and with a hole into which a pint jar could be fitted at the other end near the top. Positively phototropic insects were attracted into the jar, which was frequently exchanged for an empty one. When the rims of two jar lids were soldered together and the centers of the tops cut out, the jar with insects could be screwed into one lid and a similar jar with cyanide into the other. When the cyanide jar was kept on the bottom, the insects were automatically concentrated in it when killed by the poison. Specimens taken in this manner were in excellent condition. Insects remaining in the box were killed by the introduction of a cotton plug saturated with carbon tetrachloride, after which they were picked from the debris. On cool days, when insects were too inactive to fly into the jar of the separator box, the sweepings were put into wide-mouth quart cyanide jars, and the dead specimens later picked from the debris. Some of the sweep collections were identified while the specimens were still fresh, whereas others were either layered in Cellu-cotton or preserved in alcohol for later determination. The rapidity with which a variety of insects could be taken by sweeping was unsurpassed by any other collecting method.

TABLE 9. Total numbers of invertebrates attracted to ground traps baited with molasses in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Kind of invertebrate	2 weeks before spray		AFTER SPRAY— 1 week		4 weeks		12 weeks		Population 1 week after treatment
	A	B	A	B	A	B	A	B	
Collembola	1	14	10	30	390	24	550	86	Not affected
Gryllacrididae:									
Ceuthophilus sp.	15	22	21	76	38	74	27	26	Moderately reduced
Hadenoecus puteanus	0	14	2	38	0	196	1	62	......
Carabidae:									
Euferonia lachrymosa	0	2	0	6	19	6	0	0	......
Carabus limbatus	4	2	0	0	0	12	0	0	Eliminated
Pterostichus spp.	2	10	1	4	4	4	5	6	......
Formicidae:									
Aphaenogaster treatae	10	20	1	88	2	394	25	192	Greatly reduced
Camponotus herculeanus pennsylvanicus	1	322	0	22	1	56	0	30	......
Formica fusca subsericea	14	14	0	0	8	4	1	0	......
Lasius niger	91	352	279	178	6	564	0	0	Not affected?
Tapinoma sessile	61	74	2	34	1	32	0	0	Greatly reduced?
Phalangiidae	11	8	0	4	0	8	0	0	Eliminated

TABLE 10. Total numbers of invertebrates collected per 2-square-foot sample of forest floor in areas A and B before and after area A was sprayed with DDT. Spraying begun on May 20, 1945.

Order	Area A					Area B					Population 3 months after treatment
	May 5	May 17	June 10	July 3	Aug. 23	May 2	May 12	June 10	July 3	Aug. 23	
Nematoda	3	2	2	2	25	2	1	8	22	14	......
Annelida	38	4	48	29	20	23	2	138	70	22	Not affected
Mollusca	0	1	1	0	0	0	0	0	0	3	......
Pauropoda	9	4	3	4	12	11	20	7	10	26	Not affected
Diplopoda	4	8	5	2	5	3	2	8	12	55[1]	Not affected
Chilopoda	17	21	17	2	18	6	6	17	9	15	Not affected
Symphyla	3	5	17	9	30	3	2	3	2	1	Not affected
Thysanura	5	1	5	0	7	1	6	7	1	5	......
Collembola	4,100	2,400	2,600	10,000	9,100	5,800	1,650	5,200	6,100	7,700	Increase
Corrodentia	3	7	0	4	0	1	1	6	4	3	......
Thysanoptera	0	1	3	0	1	0	1	0	1	0	......
Heteroptera	2	2	1	7	0	0	0	0	5	0	......
Homoptera	2	5	1	574	0	1	3	2	1	2	......
Coleoptera	27	34	40	53	63	51	89	41	57	79	Not affected
Trichoptera	0	0	1	0	0	0	0	0	0	1	......
Lepidoptera	16	14	10	4	19	8	31	11	5	35	Not affected
Diptera	372	142	96	102	30	193	223	371	222	86	Moderately reduced
Hymenoptera (except ants)	7	4	5	8	18	6	7	10	7	4	......
Formicidae	60	27	119	104	1	7	28	18	31	11	Not affected
Araneae	25	3	5	46	46	2	9	3	18	75	Not affected
Phalangida	0	1	0	0	0	0	0	2	0	0	......
Acarina	11,300	10,550	11,000	16,800	17,900	8,200	12,300	14,500	14,100	18,600	Not affected
Pseudoscorpionida	17	4	12	16	94	8	28	12	18	92	Not affected
Protura	23	14	20	1	28	9	22	12	13	23	Not affected
Totals	16,033	13,254	14,011	27,767	27,417	14,335	14,431	20,376	20,708	26,852	

[1] Attributable to inclusion of a newly hatched mass of eggs.

Ground Traps

Each ground trap consisted of a pint fruit jar embedded in the soil. The soil around the top was smoothed so that any ground insects attracted by the bait could easily get into the jar. A tripod of short sticks arranged around each jar supported a flat rock which protected the jar from rain. One set of jars was about one-fourth filled with fish (herring), and another set about one-fourth filled with molasses. The traps of each set were spaced about 100 yards apart. To avoid trapping out the insect population attracted to the rotten fish before the spray was applied, examples of the species caught were kept for identification and the rest liberated after counting at a distance of 100 yards from each trap site.

Eight traps baited with fish and eight baited with molasses were used for each sampling period in area A and four of each in area B. The traps were set for 3- or 4-day periods, once before area A was sprayed and again 1, 4, and 12 weeks afterwards. The number of insects taken in the control traps was doubled for comparison with those captured in the sprayed area. There was great variation in the number of specimens taken per trap.

Similar numbers of traps were set in areas D and E a week before the spraying, and both areas were trapped again a week after spraying. Only records for four traps were available for the first measurement in area D, since the others were raided by predators.

The fish traps were malodorous; so that specimens were taken out with long forceps and rinsed several times before being preserved in alcohol. Insects in the molasses traps were strained out with a piece of fine-mesh screening, then washed several times with water before being preserved. The most abundant insects captured in the ground traps are listed in tables 8, 9, 15, and 16.

Berlese Funnels

Modified Berlese funnels were used in studies of fauna of litter, leaf mold, and organic soil at 4 stations in area A and at comparable stations in area B. Each station was located in a well-shaded site ranging from a moderately dry forest of white oak and red maple to a dry chestnut oak, sassafras, red maple, and chestnut sprout complex near the top of a ridge. Sampling consisted in removing about 2 inches of litter and about 1 inch of humus down to mineralized soil. A composite of two ½-square-foot areas taken within 1 foot of each other constituted 1 sample. At the laboratory each sample was put in a modified Berlese funnel. A 100-watt electric bulb was used for the first 24 hours, after which it was replaced by a 150-watt bulb to hurry the process of forcing the organisms down through the soil into the jar with alcohol below. Each sample was allowed to remain in the funnel until no more animals fell into the jar of alcohol. The organisms were then separated from the dirt and debris, which inevitably fell through, and stored in vials containing alcohol.

TABLE 11. Total numbers and percent reduction of insects collected in light traps in areas D and E before and after area D was sprayed with DDT on June 5, 1945.

Order	May 30-June 4		June 5-12		June 13-17		June 22-July 12		Percent reduction after		
	D	E	D	E	D	E	D	E	1 wk.	2 wks.	3 wks.
Orthoptera	0	0	0	2	7	4	6	0	..	..	..
Neuroptera	0	0	0	0	1	4	1	0	..	..	..
Plecoptera	0	0	0	0	0	0	19	0	..	..	..
Heteroptera	0	1	0	0	1	7	1	0	..	..	..
Homoptera	0	0	0	1	0	36	0	17	..	..	..
Coleoptera	26	41	60	322	437	1,712	178	318	71	60	12
Trichoptera	19	23	13	29	43	62	11	5	46	16	0
Lepidoptera	290	469	94	492	182	483	296	475	69	39	0
Diptera	137	254	408	173	406	186	863	338	0	0	0
Hymenoptera	3	6	2	3	31	2	15	6	0	0	0
Totals	475	794	577	1,022	1,108	2,496	1,390	1,159	6	26	0

TABLE 12. Average numbers of selected Macrolepidoptera captured in light traps in areas D and E before and after area D was sprayed with DDT on June 5, 1945.

Species	May 30-June 4 (5)[1]		June 5-15 (8)		June 16-July 12 (7)		Population 1 week after treatment
	D	E	D	E	D	E	
Phalaenidae:							
Lacinipolia renigera	0.8	2.4	0.4	0.4	0.0	0.0	Not reduced
Lasiocampidae:							
Malacosoma americanum	4.0	11.2	7.6	1.9	0.1	3.0	Not reduced
Geometridae:							
Heterophleps triguttaria	1.4	0.8	0.2	1.6	1.1	0.8	Greatly reduced
Xanthorhoe lacustrata	7.0	13.8	1.3	3.7	0.4	3.0	Slightly reduced
Ectropis crepuscularia	0.8	0.6	0.2	1.2	0.1	0.0	Greatly reduced
Other Macrolepidoptera	5.2	8.8	3.9	5.6	8.0	7.6	Not reduced
Totals	19.2	37.6	13.6	14.4	9.7	14.4	Not reduced

[1]Figures in parentheses represent numbers of samples.

Table 10 shows a condensation of the results of 28 square-foot samples. Ordinarily two samples from a treated area and two from the corresponding check area were run concurrently in 4 funnels. During the two prespray periods, however, samples from two areas were not run concurrently, and each run consisted of 4 samples from a single area. The population figures for these earlier sample periods were adjusted to the area equivalent used for the later sample periods, and all the figures in the table represent the number of organisms found in 2 square feet of area on a given date.

All forms, except mites and Collembola, were counted. The mites and Collembola of each sample were estimated by diluting the collection preserved in alcohol to a certain volume, shaking to obtain a uniform mixture, and drawing off 1/72 of the volume for counting.

The average number of specimens per square foot for all samples was 9,759. The small size and extremely large numbers of individuals made it expedient to identify the forms by phyla, classes, orders, or families. It is possible that some results of significance are lost because of this lumping.

TABLE 13. Average daily catch and percent reduction of the most abundant species of calypterate flies taken in fly traps in areas D and E before and after D was sprayed with DDT on June 5, 1945.

Species	May 29-June 5		June 6-July 26		Percent reduction
	D	E	D	E	
Pyrellia cyanicolor	83	145	8	56	75
Mydaea spp.	59	42	3	27	92
Pegomya lipsia	61	130	1	49	95
Phaenicia caeruleiviridis	12	11	1	10	91
Platycoenosia mikii	8	22	1	14	80
Total Calypteratae	485	543	36	269	85

POPULATION COUNTS

A rather dependable method of ascertaining comparative population numbers was to base estimates on the number of individuals of a species that could be collected in a given unit of time. Best results were obtained when the collector was familiar with the behavior and the microhabitats of the different species being studied. Some population studies were made by laying out quadrats, within which the numbers of certain larger insects or spiders were counted. Insect infestations (immature stages) on trees or shrubs were studied by making counts of the species confined to a web, leaf, or some other part of the host. An effort was made to obtain a good estimate of the numbers present immediately before and immediately after the spray application, and at later times.

GENERAL OBSERVATIONS

Valuable data resulted from direct observations on the abundance of particular species in the check area, as compared with their abundance in the sprayed area before and at various times after the spraying. Fragmentary information accumulated on many species supplemented that obtained from different collecting and trapping methods. In addition a frequent general reconnaissance of the areas disclosed the development of outbreaks, such as aphids and mites, and the role of biological agents and weather in the control of such epidemics.

STUDIES IN AREAS A AND B

DESCRIPTION OF AREA A

Area A is a 1,200-acre tract located in Spring Brook township, 3½ miles southeast of Moosic, Pa. It was selected as presenting the problems expected in a large-scale spraying operation, and was sizable enough to minimize the effect of repopulation from surrounding unsprayed woods after treatment. It is roughly oval, 1¼ miles wide and 1¾ miles long, including much of a small mountain rising from the 1,100-foot general terrain to an altitude of 1,800 feet. The

TABLE 14. Total numbers and percent reduction of invertebrates collected on sticky trap boards at intervals in areas D and E before and after area D was sprayed with DDT on June 5, 1945.

Order or family	May 28-June 4		June 8-14		June 14-25		June 25-July 9		Percent reduction after—	
	D	E	D	E	D	E	D	E	1 week	4 weeks
Collembola	5	3	1	5	2	8	5	10	..	..
Orthoptera	0	1	1	4	3	3	1	0	..	..
Isoptera	0	0	0	1	0	0	0	1	..	..
Neuroptera	0	0	0	0	3	0	0	0	..	..
Corrodentia	0	0	0	0	1	20	82	81	..	..
Thysanoptera	15	21	45	25	70	98	68	98	0	3
Heteroptera	5	4	2	6	3	11	12	8	..	..
Homoptera:	310	293	69	345	511	975	2,054	3,482	81	44
Aphidae	87	120	140	144	308	157	387	167	0	0
Coleoptera:	300	247	117	203	193	386	101	208	52	60
Cantharidae	82	156	37	233	209	235	315	36	70	0
Chrysomelidae	24	14	13	28	49	104	8	58	73	92
Coccinellidae	6	6	14	20	6	33	9	21	0	57
Elateridae	23	85	25	41	68	186	54	78	0	0
Cyphonidae and Ptilodactylidae	460	69	140	116	110	132	138	237	82	91
Lampyridae	1	1	8	1	24	15	48	51	0	6
Mordellidae	16	15	6	21	46	115	109	113	73	10
Staphylinidae	18	22	7	14	12	32	14	23	39	25
Mecoptera	4	4	0	11	1	44	3	24	100	87
Trichoptera	3	9	1	1	1	1	0	9	..	..
Lepidoptera	56	94	14	144	12	35	21	12	84	0
Diptera	2,103	4,120	1,127	1,518	4,067	3,392	4,403	7,117	0	0
Hymenoptera	521	880	195	1,273	818	1,280	1,049	1,211	74	0
Araneida	19	14	8	19	25	68	30	50	69	56
Acarina	3	3	2	1	7	5	9	5	..	..
Totals	4,061	6,181	1,972	4,174	6,549	7,335	8,920	13,100	28	0

TABLE 15. Total numbers and percent reduction of ground-inhabiting Coleoptera attracted to ground traps baited with fish in areas D and E before and after area D was sprayed with DDT on June 5, 1945.

Species	Week before spray (4 traps)		Week after spray (8 traps)		Percent reduction in area D
	D	E	D	E	
Carabidae:					
Chlaenius aestivus	0	3	1	6	..
Silphidae:					
Nicrophorus orbicollis	39	29	23	78	78
Nicrophorus tomentosus	0	0	3	4	..
Prinochaeta opaca	0	2	12	4	0
Silpha inequalis	3	6	5	0	0
Silpha noveboracensis	2	5	118	118	0
Staphylinidae:					
Aleochara spp.	2	0	3	2	..
Ontholestes cingulatus	4	5	1	0	..
Philonthus cyanipennis	0	0	9	14	..
Staphylinus maculosus	1	0	2	2	..
Tachinus fimbriatus	0	0	4	6	..
Tachinus spp.	0	0	4	2	..
Histeridae:					
Hister spp.	1	0	12	4	..
Scarabaeidae:					
Onthopahgus hecate	0	0	4	0	..
Onthophagus janus	0	0	5	0	..
Other Coleoptera	4	3	7	18	..
Totals	56	53	213	258	22

humus is thin, and the soil rocky and well drained. Most of the area supports a moderately dense growth of saplings up to 6 inches d.b.h. The dominant trees are red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.), with northern red and chestnut oaks (*Quercus borealis* Michx. and *montana* Willd.), sassafras (*Sassafras albidum* (Nutt.) Nees), and largetoothed aspen (*Populus grandidentata* Michx.) interspersed. A few large trees, mostly oaks, pitch pine (*Pinus rigida* Mill.), and black gum (*Nyssa sylvatica* Marsh.), survived former fires and are scattered throughout the area. A low, dense growth of scrub oak (*Quercus ilicifolia* Wang.) covers the dry crest of the mountain.

The undergrowth is largely of ericaceous shrubs. Blueberry (*Vaccinium angustifolium* Ait.) and Wintergreen (*Gaultheria procumbens* L.) cover a large part of the forest floor, and both sheep and mountain laurels (*Kalmia angustifolia* L. and *latifolia* L.) are abundant. Also common are witch hazel (*Hamamelis virginiana* L.), hazel-nut (*Corylus rostrata* Ait.), and mapleleaf viburnum (*Viburnum acerifolium* L.). On dry slopes are large patches of huckleberry (*Gaylussacia baccata* (Wangh.) Koch) and sweet-fern (*Myrica asplenifolia* L.). The dominant herbs are bracken (*Pteridium aquilinum* Kuhn.) and wild sarsaparilla (*Aralia nudicaulis* L.).

A valley containing a small stream extends from near the center of the area north to the boundary. A trail was cut through this valley, and the majority of the observations and collections were made in this

FIG. 3. Partial view of area A located above highway.

region. The woods along the lower portion of the valley is moist and somewhat richer than on the dry slopes near the center of the area (Fig. 3).

DESCRIPTION OF AREA B

Area B was not treated and was used as a check for area A. It is located 1¼ miles southeast of area A and is similar in vegetation, soil, and drainage. One section matches the dry sites of the treated area; another is similar to the moist valley.

TABLE 16. Total numbers of invertebrates attracted to ground traps baited with molasses in areas D and E, 1 week before and 1 week after after area D was sprayed with DDT.

Species	Before spray D	Before spray E	After spray D	After spray E	Population 1 week after treatment
Collembola	14	16	112	106	Not reduced
Blattidae:					
Parcoblatta sp.	11	0	20	0	Not reduced
Gryllacrididae					
Ceuthophilus sp.	4	0	13	2	Not reduced
Carabidae:					
Euferonia lachrymosa	0	0	4	4	......
Chlaenius aestivus	3	4	2	10	Greatly reduced
Formicidae:					
Aphaenogaster sp.	105	8	39	64	Not reduced
Aphaenogaster treatae	0	6	143	30	Not reduced
Camponotus herculaenus pennsylvanicus	0	0	0	8	......
Formica exsectoides	60	0	168	0	Not reduced
Lasius niger	331	1,804	1,769	2,972	Not reduced
Leptothorax curvispinosus	4	0	18	0	......
Prenolepis sp.	98	600	4	500	Greatly reduced
Prenolepis imparis	200	8	0	400	Greatly reduced
Tapinoma sessile	80	4	700	90	Moderately reduced
Araneida:					
Pirata sp.	5	0	17	44	......
Leiobunum sp.	17	10	0	48	Greatly reduced

The fauna of area B is somewhat richer and more varied than that of area A, probably owing to the denser forest undergrowth and the thick marginal growth along adjacent roads and clearings. The area is somewhat cooler, the plants during May and June flowering about 4 days later than in area A.

SEASONAL DATA

In March and early April 1945 there was a period of warm and fair weather. Many plants opened early, and the season was generally advanced. For most of April and May the weather was cold, the rainfall unusually heavy, and the season retarded. Azalea and sassafras began to bloom late in April, and dogwood about May 8. When spraying was begun on May 20, the leaves of maples and aspens were almost completely expanded, those of chestnut oaks averaged less than half out, and most white oak leaves were one-quarter the full size or smaller. Blackberry started flowering in area A on May 22, sheep laurel on May 27, and mountain laurel on June 5. The foliage of most trees was fully expanded when the spraying was completed on June 1.

The average temperatures at 8 a.m. for May, June, July, and August were 52°, 61°, 66°, and 61° F., respectively, while those at 5 p.m. were 62°, 70°, 73°, and 72° F. Rainfall for the same 4 months was 7, 8, 11, and 5 inches, respectively.

SPRAY APPLICATION

Because of rainy and windy weather the treatment of area A required much more time than anticipated. Spraying of the middle 600 acres was started on May 20 and not completed until June 1, and of the periphery not until June 9. The formula per gallon of spray was 1 pound of DDT, 1 quart of xylene, and 2.82 quarts of horticultural spray oil. The solution was dispersed by 2 airplanes, a White Standard biplane equipped with a spinner disk and a N3N-3 biplane equipped beneath the lower wing with a boom bearing a series of nozzles. Boundaries and sections of the area were marked beforehand with colored windsocks fastened to the tops of tall trees. It was difficult, however, to distribute the insecticide evenly, owing partly to wind currents and to the irregular contours of the ridge. Ordinarily the pilots flew about 50 feet above the tree canopy, a hazardous undertaking in the mountains. The amount of spray emitted from the plane on area A averaged about 3.7 pounds of DDT per acre, but in certain parts ranged from 1 to 5 pounds, and small portions may have been covered twice or missed entirely. The upper part of the valley, in which most of the observations and collections were made, was treated by the N3N-3 biplane at the rate of 4 pounds of DDT per acre, whereas the lower part was treated by the White Standard biplane at the rate of 5 pounds of DDT per acre. Both these dosages are several times greater than necessary for the control of defoliating insects. On the basis of other tests, probably less than one-fourth of the DDT leaving the airplane actually reached the ground in open sites.

SPRAY DRIFT

Twice it was possible to study the effect of wind drifting the insecticide into adjacent forest lands not scheduled to be treated. The north boundary of area A was treated by an airplane with spinner disks in the early morning, in the presence of a slight breeze blowing across the line of plane flight. Directly below the plane particles of spray could be felt as they fell, and after application droplets of assorted sizes could be seen on the foliage. The presence of a few droplets was also noticed, however, more than 500 feet leeward from the line of nearest plane flight, and there was a fine oil film on a reservoir 800 feet away. According to collections from the trays placed in the untreated forest, mortality due only to drift, up to 450 feet from the nearest plane application, was about one-third as great as that in the area purposely covered.

On another day two temporary ponds 800 and 2,000 feet from the nearest plane flight gave additional data on spray drift. DDT at the rate of 4 pounds per acre was applied early in the morning. A light breeze marked by occasional gusts was blowing across the line of flight. Forty-five minutes after the spraying numerous aquatic insects on and in the nearer pond were affected or dying. Thirty minutes later tortricid caterpillars from the overhanging foliage were falling into the pond. Some flies and Collembola seemed unaffected.

The farther pond was observed 4 hours after the spray application. One margin was covered with an oil film in which large numbers of dead or dying surface-breathing aquatic insects were found. They included water beetles (*Berosus*, *Tropisternus*, and *Dineutes nigrior* Robts.), aquatic Heteroptera (*Gerris marginatus* Say and corixids), and mosquito larvae. A few aquatic beetles and heteropterons were seen alive there on the following day.

DDT DEPOSIT ON FOLIAGE AND THE INFLUENCE OF WEATHER CONDITIONS

Observations made in 1945 showed that DDT sprays dispersed by airplanes left uneven deposits on forest foliage. This condition has been attributed in part to variable air currents, the type of distributing apparatus, overlapping of swaths, and to the nature of the forest canopy. The spinner-disk distributing apparatus broke the spray into fine droplets, and left scattered patches of minute crystals on the foliage. This deposit was highly lethal lasting for almost 3 months (table 2). The multiple-nozzle distributor produced droplets of much larger size, and after the solvent and oil carrier had evaporated, crystals of DDT were readily seen on the foliage. This deposit varied considerably, sometimes even between adjacent leaves of the same tree. In some places no patches of DDT could be seen, and in other places crystals were so abundant as to give the foliage a whitewashed appearance.

Where a heavy crystal deposit was obtained on the foliage, it could be seen there for 3 months, in spite of about 24 inches of rainfall during this period. To find the amount of DDT still present on foliage 3 months after treatment, three sets of leaf samples were taken from shrubs and small trees, two in the treated area and one in the control, each within a radius of 50 feet. Leaves showing a maximum deposit of crystals were taken whenever possible. One square foot of leaf surface was collected for analysis from each of the following 6 plant species: chestnut oak, white oak, mountain laurel, witch hazel, sassafras, and red maple. After 3 months of exposure to weather, the foliage samples from the area sprayed with the spinner disk averaged 0.067 mg. of DDT per square foot, which is at the rate of 0.007 pound of DDT per acre (range 0.00 to 0.02), whereas samples from the area sprayed with the multiple-nozzle distributor averaged 0.977 mg. per square foot or 0.098 pound per acre (range 0.05 to 0.17). In both instances the spray was originally dispersed at the rate of 5 pounds of DDT per acre. The small amount recovered, even from leaves having a heavy residue of crystals, would indicate that most of the deposit was no longer DDT.

Fruit flies (*Drosophila*) were used for a biological test. With the strain used 100% mortality could be expected after a 24-hour exposure to leaves sprayed with DDT at the rate of 0.15 pound per acre. Out of 9 tests (30 flies per test) run on some of the above-mentioned oak and laurel leaves, only 2 showed a 3 percent mortality within 24 hours; after 96 hours mortality averaged 11 percent, and ranged from 0 to 37. The loss of flies in the 4 controls was less than 2 percent after 96 hours. Thus, a heavy deposit of old spray crystals on foliage is no assurance that much DDT is present or that it is still as toxic as when fresh.

DISCUSSION

To give an over-all picture of the effect of an airplane spray of 5 pounds of DDT per acre, the section of area A sprayed on May 25 will be described from the day of application until studies in the plot were discontinued. Intensive observations were made on this plot up to 3 months after the spray application, and a brief reconnaissance was made during the spring and summer of the following year.

By May 25, 1945, the leaves of red maple were fully expanded and those of white oak about one-third out. A week earlier late-spring insects had begun to emerge in numbers. The morning was cool and clear, with a temperature of 55° F. at 7 a.m., and only an occasional breath of air stirring the tops of the higher trees. Along the ridges there was a considerable breeze which would soon invade the valleys to stop the airplane swath runs from being made about 50 feet above the tree tops. Shortly after a spray run was made, one could hear the rain of fine drops striking the foliage. A few moments afterwards the mistlike portion of the spray came down, the tiny droplets being carried almost horizontally by air currents before settling on the foliage

or the ground. For a short while after the spraying for the day was completed, there was a distinct odor of xylene in the air. For several days myriads of pin-point spray droplets glistened on the foliage; the largest ones directly below the plane flights and the smaller ones on foliage up to about $1/8$ mile away showed the extent of spray drift.

As soon as the spraying for the day was completed (about 8 a.m.), trays placed to catch insects falling from trees were examined, and small caterpillars, cantharids, coccinellid larvae, cerambycids, fungivorids, tendipedids, parasitic Hymenoptera, and other insects were found. This initial fall was largely of insects hit directly by spray droplets. Most of the smaller insects in the trays were already motionless, while the rest were rapidly combing their antennae or working their legs in a stiff irregular manner. The caterpillars were intermittently twitching, squirming, or trying to crawl. All seemed to be much irritated and making a supreme effort to escape. A *Rhagio* would fall into a tray and begin slowly and awkwardly to climb up the sides. It too would soon be in its death struggles. At the bases of trees were numbers of dying insects—*Hemerobius*, *Sapromyza*, phalangids, fungivorids, small beetles, and others. Many insects of diverse groups could be seen in death struggles both on top of and crawling beneath the forest litter. Many insects were still flying about in the woods. However, when an occasional flying insect would alight, it would raise its legs one at a time, scrub its antennae, or try to walk, all in a peculiar awkward way. Some did this and would fly away again; others had alighted for the last time.

A series of small pools in a wet depression had their surfaces covered with an oily scum in which floated dead and dying small Diptera, caterpillars, and other insects. Some of the larger caterpillars had sunk to the bottom. In a pool of a nearby streamlet a number of terrestrial insects were on the bottom. Aquatic insects too were showing effects of the spray. Mature nymphs of *Leuctra* were crawling or swimming in an erratic manner. Some had become trapped in the surface film and were floating downstream. Nymphs of *Ameletus* and *Acroneuria* were struggling or swimming along the bottom, and some large caddisfly larvae were unusually active.

Observations during the next 3 days showed only about 10 percent of the conspicuous part of the arthropod fauna remaining, but with small numbers of nearly every species still alive. Many species that had been common before the spraying were found as occasional survivors or not at all, whereas others were still common. Many of the Diptera, Neuroptera, small Hymenoptera, and lepidopterous larvae were greatly reduced in numbers, whereas many species of Hemiptera, Orthoptera, Hymenoptera, Coleoptera, Lepidoptera, and Araneida had survived well up to this time, but disappeared soon afterwards.

Beginning with the day after the spraying, teneral specimens of many species were common and conspicuous. During the spraying *Panorpa latipennis* Hine and *P. submaculosa* Carp. were emerging in numbers every morning. The spray killed these insects on the wing, but for several mornings afterwards teneral adults were common. Observations in the afternoons showed that very few of each morning's hatch survived the day. Other species of insects emerging until early in July were similarly killed by the residual effect of the spray.

The numbers of flying insects reached a low of about 10 percent of their former abundance a few days after the spray, and there was no apparent recovery for at least 2 weeks (including much rainy weather), after which they began gradually to increase. Six weeks after the spraying many species had increased to one-third of their pretreatment numbers. At this time the sprayed area seemed to offer a fair chance for reproduction to many species. Before this the adults had died so quickly after emergence that it is doubtful whether a significant number of those requiring a long preoviposition period were able to oviposit. As the residual effect of the spray wore off, immigrants and many insects emerging within the area were able to survive. Then some of the parasitic and predaceous forms were taken in increasing numbers, their increase in many cases following closely that of their hosts.

All tree-inhabiting caterpillars present at the time the area was sprayed were eliminated. Caterpillars infesting low vegetation were initially reduced, but gradually became as abundant as before. Most of their hymenopterous parasites, particularly Braconidae and Ichneumonidae, became almost non-existent soon after the spray application. Members of these two parasitic families gradually increased in numbers to perhaps one-fourth of normal abundance at the end of 3 months. The larger moths did not appear to be affected, whereas the smaller species were reduced in numbers. Some of the Diptera, particularly calypterate flies, were almost eliminated shortly after the spraying and showed little reestablishment later. Tree-inhabiting chrysomelids, cicadellids, and membracids were greatly reduced by the spray, while a cercopid was unaffected. Certain other tree-inhabiting insects that were not affected included *Psylla annulata* Fitch, which feeds on the undersides of leaves; many scale insects, most of which were under protective coverings at the time the spray application was made; and Collembola, mostly species dwelling under bark scales. There was considerable evidence that certain Collembola and scale insects increased in numbers after the spraying, probably as a result of the decimation of their natural enemies.

Aphids and their enemies were present in normal numbers before the spraying, but this relationship was apparently upset, and an aphid epidemic resulted. Aphids on the undersides of leaves survived the spray, others immigrated into the area, and both groups finally settled on new growth that was not contaminated. Aphid predators (adult cantharids, mirids, lygaeids, nabids, anthocorids, and syrphid,

coccinellid, and chrysopid larvae), reduced to a low ebb by the spray, soon responded to the abundance of their hosts and built up a large population. Nevertheless, the outbreak did not subside until the aphids were decimated by a heavy rain.

Another aftermath of this spray application was a tremendous increase of a mite, *Paratetranychus unnguis* (Jac.), on foliage. This species became very abundant in August and reached epidemic numbers the following May, when it caused a distinct blotching of maple leaves. Probably the severe reduction of *Coniopteryx vicina* Hagen and possibly of other predators initiated the outbreak.

Many of the ground-inhabiting insects, including beneficial scavengers and predators, were not seriously affected. Some species, including many tendipedids, lycorids, itonidids, and fungivorids and their various hymenopterous parasites, bred abundantly in the humus and had such a short adult life that, in spite of continuous decimation by DDT, they were always common and evidently breeding successfully. Another dipterous group that survived the spray well was Drosophilidae, which was not common at the time of the spray application, but became abundant a month later. Most of the predaceous ground beetles and carrion-feeding beetles survived the spray, but a few species appeared to be eliminated. Ants were not immune to the spray, but they seemed to be little affected by the residue after the first week. They fed extensively upon spray-killed insects and the abundant honeydew in the area. At the end of the season their colonies were as numerous and populous as before the spraying.

Most of the fauna in litter, leaf mold, and soil was not affected by the spray application. There was an indication that the Diptera were slightly reduced and that there was an increase in Collembola population.

An intensive study of the spiders showed the action of DDT on them to be about the same as on insects. Species that build webs out in the open and those that run over the leaves and bark were either eliminated or greatly reduced. Most of the species living under loose bark, under stones, or in the forest litter were not affected.

ANNOTATED LIST OF INVERTEBRATES STUDIED IN AREAS A AND B

Data on the effect of DDT on the large number of invertebrates studied are given in a systematic list, either by species or by some higher category. In this way all the information from different collecting and trapping methods is summarized to give an estimate of the effect of the DDT on each organism. For the over-all effect of DDT on the forms collected in numbers by a particular field method, reference can be made to those species taken in greatest numbers by each method in the appended tables.

It was impractical to identify to species all the thousands of specimens taken in this study. That many species could be determined only to genus or to family is unfortunate, for the effect of DDT on many individual species is masked by their being included with others.

Under each order or family in the list are noted the methods used to estimate the effects of DDT on each species, and the tables listing the more abundant invertebrates. The estimate is given in general terms, such as *not reduced, slightly reduced, moderately reduced, greatly reduced, survived,* and *eliminated.* By *survived* we refer to those species upon which there are little data, but which were present in the sprayed area infrequently following the spray application. These terms particularly concern the over-all effect of the DDT application 2 weeks to 3 months after the spray application. Some specimens of almost all species were killed by the spray during the first few days after application. All measurements of insect populations were very low for several days in early June because of rains and cool weather. Less intensive observations were made for a short period in the spring of 1946, and notes on the species then afield are included. For each major group information is given on species that were least affected and those most severely affected, and reasons for this as suggested by their structure, life history, or relation to environment.

NEMATHELMINTHES

Nematoda

Small numbers were taken in soil samples. They apparently were not affected by the spray (table 10).

ANNELIDA

The worm obtained from soil samples run through the Berlese funnels was not the large form commonly known as the fishworm, but a small species seldom attaining an inch in length. The populations were about equal in both areas 3 months after treatment (table 10). Not affected.

MOLLUSCA

Snails. Small collections taken periodically in the ground traps indicated that snails, mostly *Triodopsis albolabris* (Say), were not affected by the spray.

Only a few slugs were taken in molasses traps in area A before the spraying, but about twice as many occurred there a month later as in area B, and there was an even greater predominance in area A three months after the spraying. Not affected.

ARTHROPODA

PAUROPODA

Data from soil samples suggests that these animals were not affected by the spray (table 10).

DIPLOPODA

Seven specimens of a large *Parajulus sensu lato* were found dead either on the forest floor or on the bottom of a small pool within 2 weeks after the spray application in area A. Large millipeds in general were common prior to the spraying, but could not be found in July and August. A smaller species taken in soil samples did not appear to be affected (table 10).

CHILOPODA

The numbers of chilopods from soil samples run through Berlese funnels indicated that centipedes were not killed by the spray (table 10).

SYMPHYLA

Rather small numbers of Symphyla obtained from soil samples run through Berlese funnels indicated that they were not affected by the spray (table 10).

INSECTA

THYSANURA

Thysanura were poorly represented in soil samples, but seemed unaffected by the spray (table 10).

COLLEMBOLA

Only a few specimens were found dead in the trays after treatment. Samples taken by several collecting methods showed a marked increase in numbers beginning 1 month after the spraying (tables 1, 9, and 10). Although only a few Collembola (in part *Sminthurus* sp.) were taken by sweeping in both areas before the spraying, a year later collections averaged 14 per hour in area B and 75 per hour in area A. Increased.

ORTHOPTERA

Phasmatidae

Diapheromera femorata (Say). One month after the spraying 2 specimens per hour were swept in area A and 11 in area B. In August, 4 per hour were swept in area B but none in A. Survived.

Gryllacrididae

Ceuthophilus sp. Ground traps baited with molasses indicated a moderate reduction in numbers a week after the spraying, but 3 months after the spraying collections in areas A and B were about equal (table 9). Not affected.

Hadenoecus puteanus Scudd. This species was not taken in area A before the spraying and infrequently afterwards, but abundant in area B (table 9). Survived.

Tettigoniidae

Neoconocephalus ensiger (Harr.). At least 4 specimens were heard singing in area A on the night of August 22. Survived or immigrated.

Pterophylla camellifolia (F.). On the night of August 22 this species was heard singing in the woods adjacent to but not in the spray area. It seems fairly certain that the species was eliminated by the spraying.

Scudderia sp. Five nymphs were found dead in trays within 2 weeks after the spraying. A year later, sweep collections averaged 1 specimen per hour in area A and 4 in area B. Survived or immigrated.

Amblycorypha rotundifolia (Scudd.), *Atlanticus testaceus* (Scudd.), and some undetermined tettigoniid nymphs were taken during June and August in area B only.

Gryllidae

Nemobius spp. Two species were very common in area A on the night of August 22, as indicated by their songs. Survived or immigrated.

Oecanthus angustipennis Fitch. Taken in August in area B only.

Acrididae

Melanoplus sp. Nymphs were taken in May and June in area B only.

Tetrigidae

Nomotettix cristatus (Scudd.). Nymphs were taken in June and early August in area B only.

ISOPTERA

Termitidae

Reticulitermes flavipes (Kollar). A large healthy colony was found under a stone in the middle of area A on July 12.

NEUROPTERA

Hemerobiidae

Hemerobius humulinus L. Emergence started about May 15 in area A, where this species was abundant up until the time of the spraying. Searches for specimens from shortly after spraying to July 17 revealed none. Sweep collections made the latter part of August, however, indicated equal numbers (4 specimens per hour) in areas A and B. The populations were also about equal 1 year later. This species was apparently exterminated, but repopulated during the same season.

Chrysopidae

Chrysopa lineaticornis Fitch. Three specimens were found dead in trays in area A, and 1 specimen each was swept from areas A and B, all in late June.

Chrysopa oculata Say. General observations indicated that this species was present in area A toward the end of May, increased in numbers during June, and became abundant in July and August. The increase in numbers was due probably to the increase in aphid infestation.

Chrysopid larvae were taken by tree jarring and by sweeping, the latter method averaging 7 specimens per hour in both areas in August. Adults were apparently reduced in numbers, whereas larvae were unaffected. Six trees jarred in area A in August 1946 averaged almost 2 larvae per tree.

Coniopterygidae

Coniopteryx vicina Hagen. Very abundant in area A from May 15 to the time of the spraying. It was apparently exterminated by the spray and was not found again until July 12, after which it gradually increased. Fourteen dead specimens were found in trays within 8 days after the spraying.

PLECOPTERA

Nemouridae

Nemoura sp. Three specimens were collected in trays 1 day after the spraying. Sweep collections in area A, 1 year later averaged 3 per hour.

Leuctra sp. Common along streamlets in area A just before the spraying, but absent immediately afterwards. Twenty specimens were found dead in trays during 2 weeks after treatment. Greatly reduced.

CORRODENTIA

Psocidae

A few nymphs were taken by tree jarring in area A before spraying; none afterwards. Two dead nymphs were found in trays the day of spraying.

THYSANOPTERA

Sticky trap boards showed that large numbers of thrips were present in both areas before the spray application, and that immediately afterwards the population of both areas dropped tremendously (table 6). The same trend was found for *Frankliniella tritici* (Fitch) taken in box area traps (table 7). The scanty numbers taken on sticky trap boards, and in box area traps and Berlese funnels (table 10) during the sum-

mer suggest that thrips were not adversely affected by the spray.

Hemiptera

Pentatomidae

A few specimens of ***Acrosternum hilare*** (Say), ***Brochymena arborea*** (Say), and ***Podisus*** sp. were killed by the spray, as evidenced by specimens in trays. In area A, four adults of ***Meadorus lateralis*** (Say) were swept in August and two adults of ***A. hilare*** in May 1946.

Lygaeidae

Kleidocerys resedae (Panz.). Sweep collections in August averaged eight per hour in area A and four per hour in area B, whereas the following May this species was eight times more abundant in area A than in B. Increased.

Reduviidae

Sinea sp. Within 2 weeks after the spraying 23 nymphs and adults were found dead in trays in area A, and none in area B.

Zelus exsanguis (Stal). A few specimens were taken in both areas before the spraying by sweeping and by tree jarring. Several were found dead in trays in area A. Sweep collections yielded specimens all summer, and on August 27 they averaged 4 per hour in area A and 12 in area B; the following May twice as many specimens were taken in B as in A. Perhaps slightly reduced.

Nabidae

Nabis sordidus Reut. Not taken in either area before the spraying, but rather common in sweep collections in August. On August 3, 126 nymphs and adults were swept per hour in area A and 192 in area B; later collections also were heaviest in B. Not reduced.

Anthocoridae

Orius insidiosus (Say). Four specimens were taken in each area in August.

Miridae

Hyloides harti Kngt. Sweep collections (nymphs and adults) in August averaged 14 per hour in area A and 16 per hour in area B. Not affected.

Lygus pabulinus (L.). Nymphs were jarred from red maple trees in both areas in May, but were not taken later.

Neolygus sp. Ten immature specimens were taken in trays within 4 days after the spray application.

Phytocoris sp. Small numbers were taken by tree jarring (table 1). Nine specimens were found dead in trays in area A within 6 days after the spraying. All specimens were immature. Eliminated.

Sweep collections in August indicated that *Ceratocapsus incisus* Kngt., *Phytocoris tibialis* Reut., and *Reuteria* n. sp. were common in area B, and that *Diaphnidia capitata* VanD. and *Phytocoris eximius* Reut. occurred in lesser numbers. A few specimens of ***Monalocoris filisis*** (L.) and ***Lygus oblineatus*** (Say) were taken in area A.

Cicadidae

Magicicada septendecim (L.). Several of these cicadas were heard singing in area A on June 10, and large numbers sang almost continuously all afternoon on June 18. Not affected.

Cercopidae

Aphrophora sp. Nymphs in spittle masses on a pitch pine branch were still alive 2 weeks after the spraying. Not affected.

Clastoptera proteus Fitch. Not taken until August, when sweep collections averaged 4 specimens per hour in both areas.

Philaenus leucophthalmus (L.). Between June 20 and August 21, 141 specimens were found dead in trays in area A, as compared with 1 in area B. Sweep collections for approximately the same period averaged 73 specimens in area A and 62 in area B, and sticky-trap-board collections (table 6), although meager, indicate that this species was not unduly affected by the spray.

Membracidae

Collections from trays shortly after the spraying suggest that tree-inhabiting membracids were greatly reduced, for 303 specimens of *Cyrtolobus* spp., *Ophiderma* spp., and *Telemona tiliae* Ball, mostly the first two genera, were taken dead in the trays of area A compared with 3 in area B. Sweepings yielded a few specimens in area B at the same time and later, but the family seemed eliminated from area A.

Cicadellidae

A number of cicadellids, particularly ***Erythroneura*** spp. and *Idiocerus* sp., were found dead in trays shortly after the spraying in area A. A cicadellid nymph was abundant in the grass on the ridge of area A immediately before the spraying, but the species could not be found again 3 days afterward. Species obtainable by sweeping did not make their appearance until late June or in August. Sweeps in area A averaged about 4 specimens per hour of *Forcipata loca* DeL. and Caldwell, *Balclutha punctata* (Thungberg), and ***Cicadella flavoscuta clavalis*** (McA.), whereas at least 4 times as many of the same species were captured in area B. *Scaphytopius angustatus* (Osb.), *Draeculacephala constricta* D. & DeL., *Macropsis sordida* VanD., *Osbornellus auronitens* (Prov.), and *Scaphytopius* spp. were common in area B, but absent in A. Tree jarring (table 1) and sticky trap-board collections (table 6) furnish corroborative evidence that members of this family were greatly reduced by the spray.

Achilidae

Catonia dimidiata VanD. During August, 22 specimens were found dead in trays in area A; none in B. Sweep collections of that month averaged 38 specimens per hour in area A and 49 in B. Probably not reduced.

Cixiidae

Cixius spp. A few specimens were taken in August in both areas. A sweep collection in area A on May 29, 1946, averaged 68 specimens per hour.

Psyllidae

Psylla annulata Fitch. Twenty-two nymphs and adults were found dead in trays in area A, compared with none in area B. Taken infrequently in both areas by sweeping during the summer. In May before the spraying, 73 nymphs were jarred from 7 maple trees in area A, and 18 in B; a year later the number collected was 91 and 6, respectively. The nymphs feed on the undersides of the leaves and hence were not ex-

posed directly to the spray. Many nymphs transformed to adults by June 13. Not affected.

Aphidae

Prior to the spraying of area A no attempt was made to study the aphid population specifically. Such measurements as were obtained from sweeping and sticky-trap-board collections indicated a normal aphid population in the presence of a sufficient number of parasites and predators to maintain a normal balance in numbers.

The aphid population was not immune to the effects of DDT, as was indicated by a heavy fall of aphids in the trays, particularly of *Drepanaphis acerifoliae* (Thos.) and *Hamamelistes spinosus* Shimer. The species taken more commonly than others were presumably in a migratory phase of their life cycle at the time of spraying and were thus more exposed to DDT. The nonmigratory phases tended to be protected by their sheltered position on the underside of the leaves. Furthermore, the principal forest trees were just leafing out at time of the application so that the aphids surviving the initial effects of the spray were able to settle on uncontaminated new growth.

Such nonmigratory populations as were studied in area A showed no reduction attributable to DDT. One colony on hazel continued until all individuals had matured to winged forms and then migrated. Thus the life history of this species progressed without interruption throughout the period of spray application and for about a week thereafter.

One colony of *Prociphilus tessellata* (Fitch) was just entering the second generation at the time of spraying. Two hours after the area was sprayed large numbers of first instars were crawling away from the parent clusters and gathering in new clusters on the alder. There was no evidence that they or their parents were affected by DDT. Two days after application of spray the second-generation clusters were established in a normal fashion. Twelve days later 4 of the 6 second-generation clusters were found to have been destroyed. The cause was not observed; however, since two large clusters in equally exposed positions survived, it seems probable that the destruction was the result of predation. This contention seems plausible since the alder was located within 20 yards of untreated forest. When observed on July 3, third-generation nymphs were establishing new clusters, and a large syrphid fly was hovering near one of the second-generation clusters. From this time on the population began to decline as a result of the inroads of syrphid and coccinellid larvae. By July 16 no second-generation adults were present and the third generation had been reduced by 70%. At the same time there was a heavy aphid infestation on neighboring aspen and tulip, accompanied by a heavy population of syrphid and coccinellid larvae.

Evidence of a widespread outbreak of several species of aphids was noticed first on July 8. The most prevalent aphids and their tree hosts were as follows: *Chaitophorus neglectus* H. & F. on *Populus grandidentata* Michx., *Phyllaphis quercicola* Baker and *Myzocallis punctatellus* (Fitch) on *Quercus alba* L., *Myzocallis alhambra* David. and *M. walshii* (Monell) on *Quercus borealis* Michx., *Myzocallis discolor* (Monell) and *Chaitophorus quercicola* (Monell) on *Quercus montana* Willd., *Myzocallis* sp. on *Quercus ilicifolia* Wang. and *Acer rubrum* L., *Calaphis betulaecolens* (Fitch) and *Glyphina betulae* (Kalt.) on *Betula populifolia* Marsh., *Euceraphis mucidus* (Fitch) on *Betula lenta* L., *Calaphis castaneae* (Fitch) and *Liosomaphis rhois* (Monell) on *Castanea dentata* (Marsh.) Borkh. (sprouts), and *Aphis coreopsidis* (Thos.) on *Nyssa sylvatica* Marsh. Honeydew was evident throughout area A. In most places it proved difficult to find a leaf on which some honeydew was not deposited. On July 12, in spite of heavy showers on the 9th and 10th, the foliage under tulip, aspen, chestnut, and occasionally beneath scrub oak, was glazed with honeydew. Syrphid adults, which appeared to be rare in the central portion of area A on the 8th, seemed to have become somewhat more numerous. Several coccinellid larvae, mostly *Anatis 15-puntata* (Oliv.), and all sizes of syrphid larvae were also seen in the central area. The predaceous mirid *Hyaloides harti* Kngt. was common throughout the area. At this time a large percentage of the aphid population was immature. The comparative scarcity of parasites and predators left only weather as a possible check on a great increase in the severity of the outbreak. An exceedingly heavy rain, amounting to 2.3 inches fell in the area during the night of July 14 and continued into the morning of July 15. From a study of the area made July 16, it seemed likely that about two-thirds of the total aphid population was beaten off the leaves and destroyed. The remaining portion was made up of a much higher than normal percentage of small nymphs, the mature individuals and larger nymphs apparently being less able to survive the washing effect of the rain. It is doubtful that the predators and, to a lesser extent, the parasites were affected as seriously.

Observations in area B and in other unsprayed areas revealed far fewer aphids than were present in area A on July 12. The only aphid present in numbers everywhere was the one on chestnut. Even this species did not show the excessively large population common on chestnut shoots in area A. In area B the last two or three terminal leaves were usually infested, while in area A the infestation usually involved four to six of the terminal leaves, with a scattered population spread generally over the plant and occasionally colonies even on the upper sides of the terminal leaves. Sweeping and sticky-trap-board collections (table 6) clearly showed a high aphid population throughout August in area A as compared with B.

Other aphids which appeared to be present in outbreak numbers were *Macrosiphum ptericolens* Patch on *Pteridium aquilinum* Kuhn. and *Cepegillettea myricae* (Patch) on *Myrica asplenifolia* L. (Sweetfern).

The aphid *Hormaphis hamamelidis* (Fitch) was exceedingly common throughout both areas. Nearly every *Hamamelis* leaf had from 1 to 6 or 8 of the conical galls.

The following May the aphid population in area A was very small, and the only honeydew noticeable was beneath a few poplar trees.

Aleyrodidae

Sticky-trap-board collections (table 6) showed that this family was moderately reduced in numbers throughout the summer as a result of the spray. Sweep collections late in May 1946 indicated that aleyrodids were present in about equal numbers in both areas, 10 to 15 insects being collected per hour of sweeping.

Coccidae

Asterolecanium minus Ldgr. About 50% of the nymphs were killed, but all the infested *Quercus montana* Willd. appeared to have an infestation greater than that present in 1944. This scale was not found in the check area.

Eriococcus azaleae (Comst.). This species showed no mortality in the sprayed area. It was not found in the check area. The infestation on all infested shrubs was much increased over that of 1944.

Chionaspis sylvatica Sanders. This species was unaffected and perhaps benefited by the spray. Several black gum trees showed an infestation that had spread to the leaves.

Lecanium corni Bouche. This scale insect seemed to have been unaffected by the DDT spray. It is more likely that it benefited from the effects of the spray. There appeared to be no mortality in the first generation in the sprayed area. Some chalcid parasitization was observed in area B; none in area A. There was some evidence that the second generation of this scale had been adversely affected by the high concentration of aphid predators that had built up in certain sectors of the area. In places it was difficult to find young *Lecanium* on the leaves. Late in May 1946 it was a rarity to see a sassafras sapling in area A that was not heavily infested with from 60 to 500 new scales. Compared with current infestations in area B and with those in area A of the year before this 1946 infestation was a definite increase.

Lepidosaphes ulmi (L.). A survey on July 12 on three hosts—*Sassafras albidum* Fern., *Acer rubrum* L., and *Acer pennsylvanicum* L.—indicated that the kill of this insect was correlated with the amount of DDT deposit visible to the eye. The kill, as represented by dead first-instar scales, ranged from 10 to 95% in area A. The greatest mortality observed in area B was not more than 10%. In the sprayed area the greatest mortality was on the old wood, and the greatest survival was in places already heavily encrusted with old scale. In the part of area A where the heaviest DDT deposit was found, the kill was nearly 100% on old growth. On the new growth, which had not been contaminated, the survival ranged from 25 to 75%.

About 30% of the gravid scales of a population of *Lepidosaphes ulmi* was found to be attacked by an egg predator mite, *Hemisarcoptes malus* (Shisner). One to 6 mites were observed under each of the scales, which were on *Acer rubrum* L. near the middle of area A.

In general the scale insects were unaffected or increased in numbers after the application of DDT in area A. Only one species, *Lepidosaphes ulmi*, seemed to have been affected adversely. Why this should have been was not clear, but probably the time of emergence of the crawlers is involved.

COLEOPTERA

Carabidae

Carabus limbatus Say. This large predaceous ground beetle was abundant in both areas before the spraying, but was eliminated from area A (tables 8 and 9).

Calosoma frigidum Kby. Several beetles were observed to have DDT tremors 6 hours or more after the spray application, and a number of dead ones were found in area A. Probably eliminated.

Euferonia lachrymosa (Newm.). This species did not appear until 1 to 3 months after the spray application, at which time it was most abundant in area A. Not affected.

Pinacodera platicollis (Say). A few specimens were taken in area A after the spraying (table 1). Survived.

Pterostichus spp. This genus was best represented by *adoxus* (Say), *mutus* Say, and *grandiceps* Lec. They were taken in ground traps (tables 8 and 9) and were more abundant in area A than in B for at least 3 months after the spray application. Probably not affected.

Silphidae

Information on this family was obtained from collections in ground traps baited with fish (table 8). The species *Catops simplex* Say appeared to be greatly reduced, and *Nicrophorus orbicollis* (Say) was practically eliminated. Another species, *N. defodiens* (Mannh.), was eliminated from area A for a time, but a few specimens were collected again 3 months later, while *N. sayi* Lap. was probably eliminated. A few specimens of *Prionochaeta opaca* (Say) occurred in area A after the spraying. Other species, *Silpha americana* (L.) and *S. noveboracensis* (Forst.), were possibly underground at the time of the spray application, for they were not taken in the traps until 1 month later, at which time they were far more abundant in area A than in B. The occurrence of dead birds immediately after the spraying and the progressive increase in dead amphibians and reptiles for the following several weeks suggests that the absence of certain silphids from the ground traps may have been due to the abundance of other carion, rather than to the silphids being eliminated by DDT. Traps set the next May, however, collected only 3 silphids in area A compared with 22 in area B.

Staphylinidae

More staphylinids were caught in ground traps baited with fish than by any other method (table 8). Meager data suggested that *Ontholestes cingulatus* (Grav.) was not affected, nor was *Philonthus cyanipennis* (F.), which was not taken until a week after the spraying. Other species that were not affected, probably because they emerged or immigrated into the area a month or so after the spray application, were *Staphylinus viridanus* Horn, *Tachinus fimbriatus* Grav., *Oxyporus femoralis* Grav., and *Palaminus* sp. Except for individuals exposed at or shortly after the time of the spray application, members of this family were probably not adversely affected by the DDT.

Histeridae

Hister sp. Fish-trap collections indicate that this form was not affected (table 8).

Lampyridae

Ellychnia corrusca (L.). Swept in small numbers from both areas in 1945 and in May 1946. survived.

Cantharidae

Cantharis spp. were common in both areas throughout the season, with a sudden peak of abundance early in August, when sweepings averaged 90 specimens per hour in both areas. Specimens were found dead in the trays of area A and about half as many in the trays of area B from immediately after the spraying until August 21, when this collection method was discontinued. Collections on sticky trap boards sug-

gest that the population in area A was somewhat reduced by the spray.

Malthodes spp. Present in both areas in June, being somewhat more abundant in area B.

Cleridae

Three specimens of *Cymatoderma bicolor* (Say) and 11 of *Hydnocera verticalis* (Say) were found dead in trays in area A within a 3-week period after the spray application.

Elateridae

Eighteen adults of *Ctenicera hieroglyphica* (Say) and three of *Sericus silaceus* (Say) were found dead in trays of area A; none in trays of area B. A few adults of the former species were taken in area A by sweeping 11 days after the spray application, and the latter species was taken in equal numbers in both areas late in May of the following year. *Athous brightwelli* (Kby.) was swept at the rate of three specimens per hour in both areas late in June. Late in May 1946 the most abundant species taken by sweeping were *Dalopius* sp. and *Agriotes stabilis* (Lec.). Probably not affected.

Coccinellidae

Adalia bipunctata (L.). Adults were common in area A in August.

Anatis 15-punctata (Oliv.). Adults of this tree-inhabiting species were common and widely distributed in area A before the spraying, some laying batches of eggs on twigs and bark, especially on white oak. Within 2 weeks after the spraying, 26 adults and 39 larvae were found dead in trays in area A, compared with 1 adult in area B. Adults of the first generation began to emerge on July 7. Small numbers of adults were captured by sweeping in both areas throughout the summer, larvae being abundant in the August 16 collections. Mature larvae, pupae, and teneral adults were common throughout area A late in August. This species was initially reduced by the spray but became abundant again, owing to a large food supply of aphids.

Cycloneda munda (Say). Adults and larvae of this species were very common in both areas in August.

Coccinellid larvae, other than *Anatis*, were killed by the spray, as evidenced by 28 specimens found in trays in area A during the first week. Although no larvae were swept in June and July, sweep collections ranged from 4 to 18 specimens per hour in August in area A, none being taken in B. A few adults of several species were observed in area A during July and August.

Alleculidae

Isomira quadristriata Couper. About twice as many adults were found dead in trays in area A as in B. A specimen was swept in area A late in May of the following year. Survived.

Scarabaeidae

Dialytella dialytoides (Fall.). Specimens were collected in area A, 1 week after the spraying (table 8). Survived.

Dichelonyx elongata (F.). Numerous specimens were found dying a week after the spray application; 31 specimens were found dead in trays. At the same time adults, apparently recently emerged, were common on foliage in area A. Probably greatly reduced by the spray.

Geotrupes balyi Jekel. This species did not become abundant until a month after the spray application and was not affected by the poison (table 8).

Onthophagus hecate (Panz.). Perhaps some specimens were affected shortly after the spray application (table 8), but the species was present in area A, 1 month later.

Chrysomelidae

Scattered collections from tree jarring, sweeping, and sticky trap boards (table 6) show that chrysomelids were greatly reduced by the spray. Counts of specimens trapped on sticky boards showed that before the spraying *Luperodes meraca* (Say) was 4 times more abundant in area A than in B, and that 5 collections in June in area B ranged from 6 to 68 specimens, whereas a total of 2 was taken in area A. Thus this species was almost exterminated. Another chrysomelid, *Xanthonia villosula* (Melsh.), was not taken until August and then in equal numbers in both areas.

Curculionidae

A few specimens of 5 species were found dead in trays in area A, and various species were taken in small numbers by sweeping in both areas throughout the season.

Scolytidae

Several specimens of *Anisandrus sayi* Hopk. and *Monarthrum mali* (Fitch) were taken in trays within a week after the spraying in area A.

MECOPTERA

Panorpidae

Two species, *Panorpa latipennis* Hine and *P. submaculosa* Carp., were abundant in area A beginning about May 20. Specimens on the wing at the time of the spraying were killed, as were also all adults that emerged later. The week after the spraying teneral specimens were seen in the mornings, but had disappeared by late afternoon. None were seen after the emergence period had passed and both species are believed to have been exterminated.

LEPIDOPTERA

Tortricidae

Argyrotoxa semipurpurana (Kft.). On May 18 the foliage of *Quercus ilicifolia* Wang. near the middle of area A was found heavily infested with this leaf roller. The larvae, which ranged from 4 to 15 mm. in length, were within rather tight leaf rolls, occasionally 2 per leaf. There was considerable defoliation. On May 20 a few larvae were crawling on leaves and stringing downward on threads. An examination of 75 leaf rolls disclosed 70 larvae. Twenty minutes after a spray run had been made 300 feet distant, downwind, about half of the larvae left the rolls. Many were very active, either dropping on threads or crawling on leaves and branches, obviously irritated by the DDT spray. Many of the writhing larvae were captured by warblers and other birds soon after they were affected by the toxicant and had left the protective leaf roll. A count of 200 rolls a day later indicated 58% mortality attributable to the spray, whereas 200 rolls examined 2 days after spray application showed 92.5% mortality. Shortly afterward no living larvae could be found. Counts in nearby unsprayed growth 2 days after the spraying disclosed 89 living larvae out of 100 leaf rolls. This species is very sus-

ceptible to DDT, for even spray drift carried by a light breeze for 300 feet or more caused about 90% larval mortality within a few days.

Large numbers of the above-mentioned species and *Archips purpurana* (Clem.), and *A. argyrospila* (Wlk.) were found dead in trays in area A, as compared with only a few of *Argyrotoxa semipurpurana* in trays in the check area.

Phycitidae

Salebria sp. Fourteen larvae were found dead in trays in area A.

Geometridae

Alsophila pometaria (Harr.). Seventy-five larvae were found dead in trays in area A; 2 in area B. Larvae were abundant on the ridge of area A, but were exterminated by spray drift even before this area was sprayed directly.

Phigalia titea (Cr.). Seventeen larvae were found dead in trays a few days after the spray application in area A; tree-jarring records indicate that the species was eliminated (table 1).

Physostegania pustularia (Gn.). Twelve larvae were found dead in trays in area A only.

About 123 larvae of 4 other geometrid species were found dead in trays in area A. Tree jarrings showed that large numbers were present before the spraying and that they were eliminated by it (table 1). A large larva common on *Vaccinium angustifolium* Ait. in area A was also eliminated. A number of geometrid larvae were taken by sweeping during the first half of August, 18 per hour in area A and 4 in B. Thus mostly tree-infested species were eliminated during the first year. Four geometrid larvae were taken by tree jarring in area A during May 1946.

Lymantriidae

Porthetria dispar (L.). Twenty-six larvae were found dead in trays in area A only. After area A was sprayed, no larvae were recovered by tree jarring (table 1) in 1945 or 1946. Eliminated.

Phalaenidae

Cosmia canescens (Behr). Larvae feeding on red maple foliage were eliminated (table 1), but adults were taken at light in area A in July (table 4).

Crocigrapha normani (Grt.). Adults were not affected by the spray (table 4).

Elaphria festivoides (Gn.). Adults may have been moderately reduced by the spray (table 4).

Epizeuxis aemula (Hbn.). Adults were abundant in both areas from June through August (table 4). The larvae occur beneath dead leaves and therefore would not be exposed to much spray.

Epizeuxis rotundalis (Wlk.). Adults were abundant in both areas and were not affected by the spray (table 4); larval habits are similar to those of species above.

Amanthes c-nigrum (L.). Moths collected at light traps showed no reduction in area A after the spraying (table 4).

Orthosia hibisci (Gn.). Thirty-five larvae were found dead in trays in area A, as compared with 1 in area B. This species was probably greatly reduced or eliminated.

Hesperiidae

Erynnis juvenalis (F.). Occurred abundantly over damp earth in trails during May in area A; less common after the spraying but still present.

Many species of tree-inhabiting caterpillars that could not be identified, or that occurred in unimportant numbers, were found dead in the trays—183 in area A and only 8 in area B—whereas dead small moths totaled 93 and 7, respectively. Sweep collections substantiate the fact that caterpillars were greatly affected by the spray, a few being taken in area A throughout the season on low vegetation, whereas from 8 to 52 specimens were collected per hour in area B. Small moths were captured throughout the season by sweeping in both areas, but at least 4 times as many were taken in area B as in A. Light-trap collections showed that adult moths were moderately reduced in numbers 2 weeks after the spraying (table 3).

DIPTERA

Diptera were collected largely by sweeping, but also on sticky trap boards (table 6), and in fly traps (table 5), trays (table 2), and light traps (table 3). The data presented on calypterate flies (Calliphoridae, Muscidae, Sarcophagidae, Anthomyiidae, and Scopeumatidae) are almost entirely from fly-trap collections. The abundance of *Bibio* and *Lycoria* larvae was estimated by examining square-yard areas of forest humus. Miscellaneous observations provided additional data.

Tipulidae

Dolichopeza carolus Alex. Adult emergence started late in June in both areas. In area A only a few teneral specimens were seen late in June, while in area B both teneral and mature specimens were seen at this time and the species was common there into July. Apparently eliminated.

Limnophila munda O. S. Before the spraying common in damp areas in the lower part of the ravine in area A. The day after this section was sprayed this species could not be found again. Apparently eliminated.

Limnophila rufibasis O. S. This species was common in moist parts of area A before the spraying. It was not collected afterwards, but disappeared from surrounding unsprayed areas shortly thereafter. The following May it was common in area B but not seen in area A. Probably eliminated.

Limonia spp. Several specimens were collected by sweeping in area A before treatment, but members of the genus were not taken again until between 2 and 3 months later, when 7 specimens were taken. Five specimens were found dead in trays from 2 weeks to 3 months thereafter. Members of the genus were taken in small numbers in area B throughout the summer. A few specimens of *L. liberta* (O. S.) and *L. gladiator* (O. S.) were collected in the sprayed area the following May. The species of *Limonia* collected in area A were *annulata* (L.) *gladiator, liberta* and *maculata* (Meig.), the first-named species being taken only before the treatment. Reduced.

Pedicia calcar (O. S.) This species was common among patches of interrupted fern (*Osmunda claytoniana* L.) in area A before treatment. One day after the spraying it was absent from places where it formerly occurred in numbers, but it was still common in surrounding unsprayed areas. It was not collected again in area A during the summer or the following May. Probably eliminated.

Prolimnophila areolata (O. S.) Before the spraying this species occurred in area A at the rate of about one specimen per 100 square feet. One day after treat-

ment only one teneral specimen was seen, and four specimens, three of which were obviously teneral, were swept 2 weeks later. Fourteen specimens were found dead in trays from 1 day to 3 weeks after treatment. The species was not collected in area A the following year, although several were taken in area B. Apparently exterminated.

Tipula spp. Specimens of *Tipula* representing 7 species were collected in area A before treatment. Nine specimens were found dead in trays from 1 to 3 weeks after the spraying. Teneral males of *T. valida* Lw. were fairly common in moist parts of area A, 1 to 2 days after treatment, and one specimen was swept 2 weeks later. Two specimens of *T. fuliginosa* Say were taken 3 weeks after the spraying. No other members of the genus were collected during the rest of the summer or the following May. The species of *Tipula* taken in area A were *cayuga* Alex., *collaris* Say, *fuliginosa*, *hermannia* Alex., *hirsuta* Doane, *senega* Alex., *trivittata* Say, and *valida*. Greatly reduced, possibly eliminated.

Several tipulids were collected in small numbers in area A immediately before treatment but not afterwards—*Dactylolabis cubitalis* (O. S.), *Limnophila emmelina* Alex., and *Erioptera hirtipennis* (O. S.). Unaffected specimens taken between 3 weeks and 3 months after application were *Elephantomyia westwoodi* O. S., *Epiphragma fascipennis*, and *Gonomyia* sp. One year after treatment *Pales ferrugineus* (F.) was common in the area; several small limoniines were also taken at that time.

The Tipulidae were greatly reduced by the treatment and several species were probably eliminated from the area. Sweep collections made between June 1-15 averaged 17 specimens per hour in area B and 1 in area A, whereas one month later they averaged 12 and 3 respectively. Probably those swept in area A during June had emerged recently, having been in the pupal stage at the time the spray was applied. During August all specimens collected, with one exception, were of the genus *Limonia*. The following May, except for two species of *Limonia*, none of the forms common the previous year were taken, and the most abundant species was *Pales ferrugineus*, which was not recorded from the area the year before.

Sylvicolidae

Sylvicola spp. Specimens of *S. alternata* (Say) and *S. marginata* (Say) were collected in small numbers in fly traps throughout the summer; much commoner in area B both before and after treatment. Survived.

Simuliidae

Prosimulium hirtipes (Fries) and *Simulium venustum* Say. In the brook in area A pretreatment samples from 10 square feet of stream bottom contained 31 *Prosimulium* larvae. No larvae were taken after the application. Fifteen adults of this family were found dead in trays from 1 to 19 days after treatment. A few were collected on sticky boards and by sweeping through the summer. Larvae probably all killed; adults immigrated into the area during the summer.

Tendipedidae

Chasmatonotus spp. Two undetermined species were common in moist parts of area A before the spraying, but only one unaffected specimen was seen afterwards, on June 6. Eleven dead specimens were taken in trays up to 2 weeks after treatment. The following May the two species were again common. Reduced, but survived in numbers.

Hydrobaeninae. Members of this subfamily were taken in large numbers on sticky trap boards and by sweeping in area A prior to treatment, and in small numbers through the summer. Collections made in area B underwent a similar but much more gradual reduction. About 230 specimens were found dead in trays in area A during the 2 months after treatment, 99 being taken on the first day; none was collected in area B. One year after the spray application hydrobaenines were collected in about half the pretreatment abundance in the sprayed area. Reduced, but partially reestablished 1 year later.

The tendipedid larvae and adults were greatly reduced by the treatment. Many specimens, mostly Hydrobaeninae, were found dead in trays for 2 weeks following the spray application. Sweeping collections dropped to almost nothing after treatment and stayed low during the summer, except for one large collection late in August made up almost entirely of *Cricotopus*.

Heleidae

Culicoides sp. One specimen was swept before and 2 within the first month after treatment. Four specimens were found dead in trays during the 3 weeks after the spraying. The species was taken in small numbers in area B throughout the summer.

Forcipomyia spp. Sixteen specimens were found dead in trays during the 2 months after treatment. The species was taken a few times by sweeping in area B but not in area A.

Sticky trap boards took 2 undermined Heleidae in area A before treatment, and 6 in area B; after treatment 3 were taken in area A, all in the third month, and 12 in B from June through August. The following May, 12 were taken in the treated area and 2 in the control. During the first 6 weeks after the spraying 4 specimens of *Atrichopogon* and 8 of *Dasyhelea* were removed from trays in area A.

No species of heleid was taken in numbers large enough to present definite evidence on the effect of treatment. Records as a whole, however, indicate that the family was probably reduced by the spray application but was reestablished 1 year later.

Fungivoridae

Boletina sp. Specimens were taken in small numbers in area A after treatment, and in large numbers in area B. Thirty-eight specimens were found dead in trays in area A, most of them late in June when the species was commonest in area B. Probably reduced.

Euphrosyne spp. *E. clara* (Lw.) was common in both areas from late in June to early in July and again late in August. During both periods twice as many specimens were taken in sweep collections in area B as in A. Nineteen dead specimens of the earlier generation were taken in trays in area A. *E. formosa* (Lw.) and one other species were taken in small numbers along with *clara*. Probably slightly reduced.

Fungivora fungorum (DeG.) This species was swept in large numbers in both areas during August. Not reduced.

Mycomya spp. In area A an average of 15 specimens were taken per hour of sweeping from late June through August, and about 100 per hour in area B. Fifty-eight specimens were found dead in trays in area A, most of them during June and early July,

when the species was most abundant in area B. Probably reduced.

Zelmira spp. Specimens were taken in equal numbers by sweeping in both areas from 2 weeks to 2 months after treatment. During the same period 25 specimens were found dead in trays in area A. At least 3 species of the genus were collected, of which *Z. genualis* (Joh.) and *Z. mendosa* (Lw.) were the commonest.

An average of 1,940 fungivorids were taken per day in fly traps in area B and 3 in area A during early July. During August these collections decreased considerably in size in area B, probably owing in part to a decrease in bait attraction, as sweeping collections in the area did not show such a reduction.

A comparison of the total Fungivoridae taken in trays and fly traps, and by sweeping indicates the following: (1) The population in the control area was low in early June, reached a peak in early July, and diminished to an intermediate level in August. (2) The population in the treated area increased gradually from early June through early July; during August it stayed relatively constant, at about one-third that in the untreated area. Sticky-trap-board collections (table 6) do not altogether support this picture, but involve few specimens. (3) Mortality from the spray was highest late in June and early July, and dropped to almost nothing in August.

Because few fungivorids were taken in May, no indications of pretreatment abundance are available for comparison, but it seems probable that the family as a whole was moderately to greatly reduced by the treatment, the population remaining low in the treated area in August after much of the residual effect of the insecticide had gone. The numbers of one species, *Fungivora fungorum* (DeG.) was apparently unaffected.

Lycoriidae

Lycoria spp. Several species were common in area A throughout the summer, although sweeping, sticky-trap-board, and box-area-trap collections (table 7) indicated the adult population was reduced considerably by the spray. Many collections after the spray application averaged only about one-fifth of that in area B until the following May. During the 3 months after treatment 482 specimens were found dead in trays in area A, 162 being taken in the first 2 days. Fifty specimens were collected over a similar period on trays in area B, but none at the time area A was treated. A survey of larvae was made 1 month after treatment by examining square-yard areas of forest humus. Twelve square-yard samples examined in each area showed 15 larval colonies in area A and 4 in area B, but those in area A averaged somewhat larger in size. Observations made on one species of *Lycoria* indicated that mating and egg laying took place soon after the females emerged from the pupae, and while they were still among the dead leaves on the forest floor. Thus the opportunity to contact the insecticide in many cases came after the eggs for a new generation had been laid. It is possibly for this reason that the insect maintained itself in numbers in area A while the adult mortality due to DDT was high. One year after treatment sticky-trap-board collections indicated that the population in the sprayed area was more than 3 times greater than that in the control area, a condition probably influenced by the reduction of parasites. The numbers of belytine Diapriidae, a group that probably parasitized species of *Lycoria* heavily before treatment, were markedly reduced in the area throughout the summer. Adults were greatly reduced but became reestablished 1 year later; larvae probably were not reduced.

Itonididae

Many specimens were taken on sticky trap boards. These collections showed a marked increase in area A over area B, beginning late in June and extending through the summer (table 6). During this period collections averaged about 3 times greater in area A than in B. Nevertheless 90 adults were found dead in trays during the 2 months following treatment, 47 of them in the first 2 days. The increase in population, in spite of what must have been a fairly high spray mortality, was probably due to the reduction of parasites by the treatment. Species of Platygasteridae and Chalcidae, many of which are itonidid parasites, showed a marked reduction through the summer.

Bibionidae

Bibio townesi Hardy. A survey of larvae of this species was made on July 3 by examining 12 square-yard samples of forest litter in each area. A total of 6 larvae were found in area A and over 1,000 in area B. In the dry upland portions of both areas, however, the populations were about equal.

Adults were collected in light traps from July 10 to August 10, the largest collections being made on July 27. During this period about 2,500 specimens were taken in area A and about 1,900 in area B. On sticky trap boards exposed from July 27 to August 2, 10 specimens were taken in area A and 76 in B. On August 2, 10 specimens were swept from area A and 66 from B. Dead specimens, 108, were taken from trays in area A from July 24 to August 14, and in area B, 202 specimens were taken from July 24 to August 21, the median in both cases falling on July 31. The mortality in the treated area, as shown by tray collections, could thus be attributed to natural causes. Not reduced.

Tabanidae

Chrysops spp. In the brook in area A, 2 larvae were collected before and one the week following treatment. One affected adult was seen the day following application. Late in June and in July *C. wiedemanni* Krb. and another species were common and annoying in the area. At least 4 species were collected. Probably not reduced.

Tabanus lasiophthalmus Macq. Four to 6 hours after the valley was sprayed many specimens that were dying could be heard buzzing in the leaves. One unaffected specimen was seen the next day, and another 3 weeks later. Three specimens were found dead in trays from 1 to 15 days after the spraying. Reduced.

Rhagionidae

Rhagio mystaceus (Macq.). Before treatment teneral specimens were common along the brook in area A. A few hours after application 12 affected specimens were seen, and 1 specimen was found dead in a tray 2 days later. The species was not seen again in the area. Reduced, possibly eliminated.

Asilidae

Asilus novae-scotiae Macq. This was a moderately common species in area A, the adults emerging about the

time of application. Several specimens were seen during the 2 weeks after treatment, all of which were teneral. During this period 6 dead specimens were found in trays. Probably eliminated.

Two affected specimens of an unidentified species were found 2 days after the spraying, and 5 other specimens were found dead in trays from 3 to 20 days after treatment. Several unaffected specimens, 1 obviously teneral, were collected in June and July. A few specimens of *Asilus, Bombomima,* and *Leptogaster* were taken in the treated area during the summer and following May.

Dolichopodidae

Members of this family were abundant in both areas, particularly in August. Most specimens were taken by sweeping; after treatment collections averaged 190 per hour of sweeping in area A, and 380 in B. Sticky-trap-board collections (table 6) also were larger in the control, and during the summer 24 dead specimens were found in trays. The following May sweeping collections were about equal from the 2 areas. Moderately reduced; reestablished 1 year later.

Empididae

Anthalia spp. During the first month after treatment 23 specimens were found dead in trays; 11 of these were *A.* new species?, taken only from June 9 to 15. A 1-hour sweep in area B on June 12 took 147 specimens of this new species?, but none were collected in area A. Probably reduced.

Noeza triplex (Wlk.) A few specimens were taken in both areas by sweeping late in June and early in August. Two dead specimens were found in trays 1 month after treatment.

Hilara spp. Fifty-four specimens were found dead in trays during the first month after treatment. More than half of these were *H. brevipila* Lw., which was taken only from June 8 to 15. On June 12, 20 specimens of *H. brevipila* were swept from area B, but none were taken in A. During August and the following May, *H. brevipila* and other members of the genus were taken in approximately equal numbers in the 2 areas. Reduced, but reestablished 3 months later.

Ocydromia n. sp.?. Ten specimens were collected in area A by sweeping before treatment, and 3 in the following 2 weeks. The species was common in area B through June, during which time sweep collections averaged 20 specimens per hour. Nine dead specimens were found in trays during the 2 weeks after the spraying. Several specimens were taken in the treated area the following year. Reduced; reestablished 1 year later.

Several undetermined species of Empididae were taken in the treated area in moderate numbers before the spraying, but in small numbers the rest of the summer. Sixty undetermined specimens were found dead in trays during June and early July. The total Empididae taken both on sticky trap boards (table 6) and by sweeping averaged about 10 times larger in the control area than in A from June through August, but in the following May empidids were back in area A in approximately pretreatment numbers.

Musidoridae

Musidora dubia (Curr.). A few specimens of this species were collected by sweeping throughout the summer and the following May, approximately equal numbers being taken in both areas. Four specimens were found dead in trays during the 2 weeks after treatment. Probably not reduced.

Phoridae

Both sticky-trap-board (table 6) and sweeping collections indicate that phorids were several times more abundant after treatment in area B than in A, particularly in July. Sweeping collections in area A averaged 75 specimens per hour from June through August, and over 300 per hour in area B. A total of 15 dead specimens were found in trays in the sprayed area during the 2 months after treatment. The species *Borophaga femorata* (Meig.) was not taken abundantly in box-area samples until June 29 and later, and probably was not affected by the DDT residue (table 7). Species of *Megaselia* were greatly reduced in numbers 2 weeks after the spraying, but almost equal numbers were collected in box area traps in both areas 6 weeks and 3 months after the spraying. The following May sweep collections of phorids in area A were still slightly below pretreatment numbers. Moderately reduced; still slightly reduced 1 year later.

Dorilaidae

Dorilas spp. Specimens of 5 different species were common in area A around *Kalmia* and other shrubs up to the time of spraying. After treatment collections by sweeping and on sticky trap boards totaled 20 specimens in area B through the summer, but only 1 specimen was taken in area A, in late August. Nine dead specimens were found in trays during the 2 months after application. Species in this genus were almost eliminated through the combined effects of the spray and the lack of cicadellid hosts.

Syrphidae

Syrphus spp. Several species were common to abundant in the treated area in July and August. Ten specimens were found dead in trays.

Xanthogramma flavipes Lw. This species was common in the treated area in mid-June, becoming abundant in July and August. One dead specimen was found in a tray 1 month after treatment.

Other syrphids collected several times in area A were *Rhingia nasica* Say, *Volucella vesiculosa* (F.), *Microdon megalogaster* Snow, and *Sphaerophoria cylindrica* (Say). Six dead undetermined syrphids were collected in trays from June through August.

Syrphid larvae associated with aphids were common in area A during July, becoming abundant in August. During the latter month sweep collections averaged 22 larvae (mostly *Metasyrphus*) per hour in the treated area and only 3 per hour in the check area.

The Syrphidae as a whole were temporarily reduced by the treatment, although no data as to the degree of the reduction were obtained. Within 3 weeks after treatment they were back in the area in numbers approximately comparable to surrounding unsprayed sections, probably owing largely to repopulation from outside the area. By August both larvae and adults became more numerous than in untreated sections. This increase was probably due in part to a reduction in their hymenopterous parasites during June, but mostly to the marked increase in the aphid population during July and August. Diplazonine ichneumonids—important syrphid parasites—were reduced only temporarily by the treatment, but possibly long enough to allow an increase in the host population. In August and the following May, however, diplazonines and

Ethelurgus syrphicola (Ash.)—another ichneumonid parasitic on syrphids—were more abundant in the sprayed area than outside. One year after treatment the syrphid population was not noticeably larger in area A than in surrounding areas.

Calliphoridae

Calliphora spp. The number collected dropped 75% during the first week after the spraying, but averaged only about a 25% reduction during June and July (table 5). This apparent decrease is of doubtful significance because of the irregularity of the data involved. One year after application no reduction was shown over pretreatment abundance. The *Calliphora* collected were about 60% *vomitoria* (L.), 30% n. sp., and 10% *vicina* R.D. A few specimens of *C. terraenovae* Macq. were taken. These species were apparently reduced immediately after the spraying, and possibly throughout the summer, but survived in large numbers.

Cynomyopsis cadaverina (R.D.) In the 3 weeks before treatment 40 specimens were taken in area A and a similar number in area B. After the spraying 3 specimens were taken in area A late in June but none in area B the rest of the summer. The following May the species was again taken in equal numbers in both areas.

Phaenicia caeruleiviridis (Macq.). Only 2 specimens were taken in area A, in late June and early August; about 100 specimens were collected in area B, from late May to early July.

Phormia regina (Mg.). The population was reduced an average of 54% by the spray during June and July (table 5). No specimens were taken the first 8 days after the spray application. Two dead specimens were found in trays, 1 day and 1 month after treatment.

Muscidae

Muscina assimilis (Fall.). Collections dropped about 26% after the spraying, a decrease of doubtful significance because of the irregularity of the data (table 5). This was the dominant calypterate species in both areas during July and August. Possibly reduced but survived in large numbers.

Pyrellia cyanicolor (Ztet.). The population was reduced 99% by the spray (table 5). This was a dominant species in area A before application, but only 5 specimens were taken in June and July as against 1,500 in the check area. They were swept in numbers in both areas in August. In the following May no specimens were taken in area A, as against about 50 in area B. Greatly reduced.

Sarcophagidae

Sarcophaga spp. About 25 specimens were taken through June and July in each area. These species probably were not attracted to the bait used as readily as related families. Three dead specimens were found in trays during the first month after treatment. Possibly not reduced.

Anthomyiidae

Anthomyia oculifera Big. A few specimens were taken in area A in May, June, August, and the following May; in area B a few specimens were taken in May and August. Survived.

Fannia canicularis (L.). During May, 30 specimens were taken in the sprayed area as against 160 in the check area. After the spraying this species was collected only twice in area A, whereas 350 specimens were trapped in B during July. These figures indicate a 94% reduction in the sprayed area, but are of doubtful validity owing to the small numbers involved (table 5). Probably reduced.

Fannia manicata (Mg.). Specimens were collected in numbers in both areas from May 15 through July, the population showing no reduction by the spray (table 5). Not reduced.

Fannia scalaris (F.). Two specimens were taken in area A before the spraying, and 20 the following month. In area B, 1 specimen was taken before, and about 300 the month after treatment.

Hydrotaea dentipes (F.). An average of 7 specimens per day were taken for 5 weeks after the spraying. The species was eliminated for 8 days after application, but the average catch for June and July showed no reduction (table 5).

Hylemya cilicrura (Rond.). This species occurred in large numbers before the spraying. After application the population was reduced by more than 99% (table 5). It was taken in numbers in area B during June and early July. Ninety dead specimens were found in trays during the 2 months after treatment. Greatly reduced.

Limnophora arcuata St. During the 3 weeks before the spraying 30 specimens were taken in the sprayed area and 60 in the check. In the 5 weeks after the spraying 35 were taken in area A and 360 in area B. This indicates a slight reduction, but results are inconclusive.

Pegomya lipsia (Walk.). This species was moderately common before the treatment, when 45 specimens were taken. After the spraying 6 specimens were collected on June 18 but none later. The species was common in area B throughout May, June, and July. Reduced.

Phaonia apicata Joh. Twenty-five specimens were taken in area A in the 2 weeks before treatment, and 7 in the 3 months afterwards. In area B about 150 were taken before, and about 700 in the 3 months after treatment. The following May, 31 specimens were collected in area A and 123 in area B; thus no reduction was shown over pretreatment abundance. Reduced but present in usual numbers a year later.

Scopeumatidae

Scopeuma furcatum (Say). Eighty specimens were taken in area A before the spraying but only 3 afterwards, these on June 27. Rather common in area B, where 180 specimens were taken in May and 120 in June to early July. Reduced. One year after treatment 10 specimens were taken in area A, 24 in B.

Several calypterates were taken in insufficient numbers to indicate the effect of the treatment on them. The following species were collected in area A during the 3 months after treatment: *Dendrophaonia hilariformis* (St.), *Fannia fuscula* (Fall.), *Helina lucorum* (Fall.), *Hylemya alcathoe* Wlk., *Muscina pascuorum* (Mg.), *Mydaea flavicornis* Coq., *Mydaea ancilla* (Mg.), and *Myospila meditabunda* (F.).

The calypterates as a whole showed approximately a 72% reduction in numbers through June and July in the area treated. During August the catches were too small to be of value. The immediate effect of the spray was obscured by about a week of cool and rainy weather just before and after application. During

this inclement weather few specimens were collected in either area. Catches were heavy in both areas during most of May. During the latter part of June catches were again large in area B, but remained low in area A throughout the season. Four species—*Phormia regina, Muscina assimilis, Hydrotaea dentipes,* and *Hylemya cilicrura*—were eliminated for an 8-day period after the spraying, but returned in some degree on the ninth day. There was no evidence of a gradual reestablishment of affected species in the treated area. Rather, during August catches in the check area decreased until they were of the same level as those from the sprayed area. This reduction may have been due to a decrease in bait attraction rather than to an actual falling off of the population.

Eight species were collected in sufficient numbers to provide definite information on the effect of the spray (table 5). On the basis of these species it is clear that, while the calypterates in general decreased, the population of certain species was diminished little if at all. These forms included *Hydrotaea dentipes, Fannia manicata,* probably also *Calliphora* spp., and *Muscina assimilis.* Forms greatly reduced (90% or more) included *Pyrellia cyanicolor,* and *Hylemya cilicrura. Phormia regina* was intermediate with a 54% reduction. Indications from a smaller amount of data showed that *Limnophora arcuata, Pegomya lipsia, Fannia canicularis,* and *Scopeuma furcatum* were probably also reduced.

Sphaeroceratidae

Copromyza equina (Fallén). During the month following treatment this species was swept in small numbers from area A and in slightly larger numbers from area B. The following May a few specimens were taken from both areas. Survived.

Leptocera spp. An average of 8 specimens per hour was swept from area A throughout the summer, and an average of 20 per hour was taken from area B. Small numbers taken in box-area samples suggested a moderate reduction 2 weeks after the spraying, whereas 3 months after treatment they were about equally abundant in both areas. Probably reduced. One year after treatment the genus was taken in about equal numbers from both areas.

Lauxaniidae

Homoneura spp. Both sweeping and sticky-trap-board collections were much larger in the control than in the treated area, although specimens were taken in area A throughout the summer, becoming slightly more numerous late in August. Sweeping collections after treatment averaged 5 specimens per hour in area A and over 100 per hour in area B. Collections on sticky trap boards totaled 19 specimens in area A from June through August, and about 500 in area B. Seventeen dead specimens were collected in trays. Species of *Homoneura* taken were *compedita* (Lw.), *ornatipes* (Johns.), and an undescribed species. Reduced.

Minettia spp. Sweeping collections averaged about 7 times larger in area B than in A throughout the summer. In area A, 22 dead specimens were found in trays during the 5 weeks following treatment, 19 being taken in the first 2 days. The following May sweep collections again averaged 7 times larger in area B. Species of *Minettia* collected were *americana* Mall., *glauca* (Coq.), *lupulina* (F.), and *obscura* (Lw.). Reduced.

Lauxaniella sp. This species was swept from both areas in August, in numbers 10 times larger from area B than from A.

Pseudogriphoneura sp. In August, 5 specimens per hour were swept from area A and 195 from B.

The Lauxaniidae were much more numerous in the control than in the sprayed area for at least 1 year after treatment. Since specimens were collected only in small numbers before the spraying no indication of the degree of mortality was obtained. The number of dead specimens found in trays, however, indicates that the low population in area A was due in part to the effects of DDT.

Sepsidae

Sepsis sp. This species was taken in small numbers in area A before and 1 month after treatment.

Chloropidae

A few chloropids were taken throughout the summer in area A by sweeping. One year after treatment *Oscinella soror* (Macq.) and *O. carbonaria* (Lw.) were common in the area.

Agromyzidae

Agromyza spp. Specimens were moderately common in the treated area throughout the summer, and slightly less common in the control. Collections were largest in area A in August and the following May. Eight dead specimens were found in trays up to 5 weeks after treatment. At least 3 species were collected, the commonest of which was *A. angulata* Loew. Not reduced.

Sciomyzidae

Specimens were taken in moderate numbers during August by sweeping, the collections from the two areas being approximately equal.

Heleomyzidae

One specimen was swept from area A before treatment, and none afterwards; two were collected in area B in August. During the first month after treatment 9 dead specimens were found in trays.

Drosophilidae

Drosophila inversa Walker. Box-area-trap samples taken over a 3-month period showed that this species was not affected by the spray (table 7).

Drosophila transversa (Fallén). This species was common in area A, particularly in August, when sweep collections averaged 65 specimens per hour. In area B collections averaged about 5 times larger. Probably not reduced.

Chymomyza amoena (Loew). This species was swept in small numbers in both areas throughout the summer, becoming moderately common in August. Two specimens were found dead in trays during the week following treatment. Box-area-trap collections suggest that this species may have been reduced in numbers after the spraying, but if so the population assumed prespray numbers about a month later (table 7).

Scaptomyza adusta (Loew). This was a common species taken in about equal numbers in both areas. Not reduced.

The Drosophilidae were only slightly if at all reduced by the treatment, and large numbers were present in the sprayed area during the summer. They were not common at the time of application, but became abundant 4 weeks later. A total of 12 specimens were

found dead in the trays of area A from 1 day to 2½ months after treatment. Drosophilids were taken in large numbers in the fly traps of both areas during July and August, but since eggs and larvae were found in the bait pans some specimens developed within the trap. For this reason fly trap data are not used.

Otitidae

Pseudotephritis vau (Say). This species was collected in fly traps in much larger numbers in area B than in A, both before and after treatment. In August fewer specimens were taken in the check area, so that collections then were approximately equal. A total of 44 specimens were taken throughout the summer in area A and 176 in area B. Survived.

HYMENOPTERA

Information on the effects of DDT on this group of insects, particularly the parasitic forms, was obtained largely from sweeping, sticky trap boards (table 6), box area traps (table 7), and trays (table 2). Data for the larger ichneumonids are nearly all from general collections and irregular sweep-net collections. Particular attention was given to the Ichneumonidae so information on this family is fairly complete.

Xiphydriidae

Xiphydria sp. One specimen was collected before treatment in area A, and 2 were taken afterwards, 2 weeks and 2 months after treatment. One week after the spraying 2 dead specimens were found in trays.

Pergidae

Acordulecera dorsalis Say. This was the commonest sawfly in area A immediately before the spraying. Two days after treatment 3 unaffected specimens were taken by sweeping. The species was not taken again in either area until the following May, when it was again a common species. Survived.

Tenthredinidae

Strongylogaster spp. Two species were common in area A before treatment, but were not collected afterwards. One of these was *S. annulosus* Nort.

A few undetermined sawfly larvae were swept from area A before treatment, but larvae were not taken again in the area until late in August, when two more were collected. Eight dead larvae were found in trays, all the first 4 days after treatment. A few larvae were swept from area A, 1 year after treatment. In August and during the following May a small number of tenthredinid adults were swept from both areas. Sawfly larvae were reduced by the treatment. Adults were taken in numbers too small to indicate the effects of treatment.

Braconidae

Opiinae and Alysiinae. Immediately following treatment the numbers were extremely reduced in area A but gradually increased until by August an average of 38 specimens per hour were swept from the treated area, as against 137 from the check area. Some of the species collected probably were parasites of agromyzid flies, a group that was little affected by the treatment. Moderately reduced.

Aphidiinae. Eleven specimens were found dead in trays during the 3 weeks after the spraying, 9 of which were of the genus *Aphidius*. A few specimens were swept in area A during the first month after treatment, and during August specimens were collected in numbers only slightly below those from area B. The reestablishment of the aphidiinae in area A was probably aided by the rapid increase in host numbers, the aphid population occurring in outbreak numbers in the treated area in July and August. Reduced, but reestablished in almost normal numbers 2 months later.

Microgasterinae. Seven dead specimens were found in trays during the 2 months after treatment, 5 of which were *Apanteles*. During August sweep collections averaged 6 specimens per hour in area A and 28 per hour in B. Reduced.

Sigalphinae (other than *Chelonus*). A few specimens of *Sigalphus*, *Urosigalphus*, and *Phanerotoma* were swept from both areas in August. The numbers were too small to be of significance, but collections were slightly larger in area A. Two dead specimens of *Phanerotoma* were found dead in the trays of area A in June and July.

Chelonus rufiscapus Prov. This species was common over all the sprayed area during July and August. Fifty-two specimens were collected in a half-hour sweep on August 2. Probably not reduced.

A few specimens of *Microbracon* and *Rogas* were swept from area A in August. Dead specimens of Euphorinae, *Heterospilus*, *Macrocentrus*, *Meteorus*, *Microbracon*, and several undetermined species were found in trays during the 2 months after treatment.

Sweeping and sticky-trap-board collections (table 6) indicate that braconids as a whole were reduced to about one-fifth of normal numbers during June, and from that low ebb increased to about one-third normal in August. The following May they were collected again in pretreatment numbers.

Ichneumonidae

Anomalon reticulatum (Cr.). Specimens were found to be common along the mountain ridge of area A on July 12 and August 28. This is a species that emerges late. Parasitic probably on Elateridae.

Astiphromma pectorale (Ash.). Specimens were common in moist parts of area A before treatment, but were not found afterwards. Outside the treated area it was moderately common until mid-June. Exterminated. A secondary parasite.

Coccygomimus aequalis (Prov.). This species was common before treatment in area A, but was not taken again until August, when 5 males were collected. Outside the treated area it was abundant and widespread. Exterminated but repopulation took place the same season. Parasite of Lepidoptera.

Coelichneumon maurus (Cr.). This was a moderately common species before treatment, but it was not seen afterwards in the sprayed area. In surrounding sections it was present in like numbers through the first week in July. Exterminated. Parasite of Lepidoptera.

Coleocentrus rufus (Prov.). Specimens were moderately common before treatment, but were not seen again until the following May, when several more were taken. Parasite of wood-boring Coleoptera.

Cratichneumon spp. One specimen of *C. quintilis* (Vier.) was swept from area A on June 11; one of *C. w-album* (Cr.) was collected near the edge of area A on June 28; and one of *C. paratus* (Say) and 3 of *C. ericaeus* Tow. were taken in August. These three latter species were common or abundant outside of the treated area throughout the summer. Severely reduced. Parasites of Lepidoptera.

Delomerista novita (Cress.). A few specimens were col-

lected before treatment, but no others were seen until the following May, when another specimen was taken. Parasite of sawflies.

Diplazon laetatorius (F.). Specimens were not collected in area A before treatment, although the species was common in adjacent sections. Seven dead specimens were collected in trays from late in June through August. The species was found to be common and widespread in the sprayed area on July 8, and later became very abundant, more so than in untreated areas. By late August its numbers had declined. One specimen was swept from area A the following May. This is a parasite of Syrphidae, and its appearance in numbers in area A corresponded with an abrupt increase in the abundance of its hosts.

Diplazon tetragonus (Thbg.). One specimen was taken in area A on July 14. In August this species became much more abundant in the treated area than in surrounding sections, sweep collections taking an average of 27 specimens per hour in area A and only 3 per hour in B. Both in August and the following May this was the most abundant ichneumonid in the sprayed area, its large numbers being correlated with the large syrphid population.

Ethelurgus syrphicola (Ash.). This species was collected only in area A in August and the following May. During the latter period it was one of the commonest ichneumonids in the area. The abundance of this species closely parallels that of the aphid-feeding syrphid flies that are its hosts.

Eusterinx compressa (Cush.). This was the only ichneumonid collected in any numbers in the sprayed area during the first month after treatment. Collections were erratic, but the numbers swept from area A were about one-tenth of those from area B in June, rising to approximately one-half the check area level in August. The following May, 7 specimens were swept from area A, none from area B. Survived. Parasitic probably on Fungivoridae.

Plectiscinae (other than *Eusterinx*). Specimens were moderately common in area A before the spraying, but during June the numbers in sweep collections were only one-tenth of those from area B. Three dead specimens were taken in trays the day after treatment. Plectiscines became common in both areas in August, but collections from area B were still about 4 times larger than those from A. In August *Proclitus, Symplecis* and *Aperileptus* were the most abundant forms. The next May, 19 Plectiscines were swept from area A, none from B. Survived. Parasitic probably on Fungivoridae.

Orthocentrus spp. Two weeks after treatment 2 specimens were swept from area A and 1 from B. In August, 6 specimens were swept from area A and 11 from B. Three species were collected, of which *O. pusillus* (Walsh) was the commonest. Survived. Parasitic probably on Fungivoridae.

Ichneumon irritator F. Several specimens were seen in area A before treatment and one a few hours afterwards; no others were seen in the area. In surrounding sections the species was moderately common throughout the summer. Exterminated. Parasitic on coleopterous larvae in wood.

Ischnus atricollaris (Walsh). This species was common before treatment, but was not found afterwards. It was common outside the treated area throughout the summer. Exterminated. Parasite of Lepidoptera.

Itoplectis conquisitor (Say). A single specimen was collected May 20 in area A before the spraying, none afterwards. During the summer this species was generally distributed in surrounding untreated areas. Exterminated. A parasite of Lepidoptera.

Mesochorus spp. Specimens of *M. hamatus* Tow. and of an undescribed species were abundant in the sprayed area up to the time of treatment. One unaffected specimen was collected 2 days after the spraying, and 3 dead specimens were found in trays during the first 3 days. The species were not taken again until the next May, when both forms were swept from area A in small numbers. Secondary parasites.

Mycrsia laminata Vier. This species was common before the spraying, and was taken again in small numbers 2 weeks, 1 month, and 2 months after treatment. Collections of the species from area B were irregular, but averaged slightly larger.

Phaeogenes spp. Two species, *P. mellinus* (Prov.) and an undescribed species, were common in area A before treatment. During the 2 days after the spraying 2 unaffected specimens were seen, but none were found again in the area. Outside the treated area both species were moderately common throughout the summer. Exterminated. Parasites of Lepidoptera.

Pseudamblyteles sp. Specimens were moderately frequent in area A from July 14 to 27. Adults of this species emerge only in July. Parasite of Lepidoptera.

Syrphoctonus spp. Specimens were common in area A in August and the following May. They were not taken in area B, but members of the genus occurred throughout the summer in adjacent areas. In August 7 dead specimens were collected in trays. The commonest species collected was *S. agilis* (Cress.). Parasitic on syrphids.

The following ichneumonids were collected more than once by sweeping in area A between 1 and 3 months after treatment: *Campoplex hyalinus* (Prov.), *Campoplex* sp., *Callidiotes* sp., *Gelis obscurus* (Cr.), *Mastrus* sp., *Otacustes crassus* (Prov.), and *Promethes* sp.

Most species of ichneumonids were severely affected by the spray and many seemed exterminated. Recovery was slow. An analysis of survival and repopulation by host relationships is revealing. Parasites of Diptera that were not greatly affected by the spray, especially of Fungivoridae, Itonididae, and Syrphidae, were moderately reduced or showed an increase over those in the control area. Parasites of caterpillars, as well as the caterpillars, were practically eliminated from the sprayed area, and repopulation was very slow. Two and 3 months after the spraying there was a noticeable increase in ichneumonid parasites to possibly 20% of normal at the end of 3 months. Probably most of this recovery was due to the replacement of hosts within the treated area and the immigration of parasites from surrounding untreated forest.

Diapriidae

Specimens were moderately common in area A before the spraying, but none was taken either on sticky trap boards (table 6) or by sweeping during the 2 weeks following the application. A species of *Xenotoma* taken in box area traps (table 7) apparently was greatly reduced in numbers by the spray, but shortly afterwards became quite plentiful. The numbers on sticky trap boards and in sweep collections increased gradually during June and July, becoming about half of normal late in August. The following

May sweep collections from area A were almost twice as large as those from the check area. This increase roughly parallels the increase in lycoriid flies, perhaps the most important hosts of diapriids in the area. Specimens collected were almost entirely of the subfamily Belytinae. Greatly reduced, but increased to more than pretreatment numbers 1 year later.

Platygasteridae

Members of this family were common before treatment. The initial mortality was high, 17 dead specimens being taken in trays, all but 2 of which fell the first day. A species of *Leptacis* taken in box area traps appeared to be reduced in numbers by the spray (table 7). The numbers in sweep and sticky-trap-board collections from area A (table 6) were very low in early June, but increased throughout the summer. In August they were about one-third as large as those from area B, whereas the following May the populations of the two areas were almost equal. Itonidid flies—hosts of platygasterids—survived the treatment in numbers, becoming very abundant following the initial reduction of their parasites. This large itonidid population probably helped the parasites in reestablishing their numbers.

Calliceratidae

Specimens were moderately common before treatment. Sweep collections were small and irregular, but collections on sticky trap boards (table 6) indicate a reduction in June and July and a partial reestablishment in August.

Serphidae

Serphidae were taken in very small numbers in both areas throughout the summer except late in August, when 21 were taken in one collection from area A.

Cynipidae

Specimens were abundant in area A in May, and were greatly reduced by the spray. A total of 143 dead specimens was taken in trays during the 2 months after treatment, 68 of them in the first 10 days. Sweep collections showed recovery to about two-thirds of normal in August, and the next May both sweep and sticky-trap-board collections (table 6) were more than 5 times larger in area A than in B.

Chalcidoidea

Many chalcids were taken on sticky trap boards (table 6) and in sweeping in area A prior to the spraying. Fifty were found dead in trays during the 2 days after treatment, and 16 more in June and July. In June the numbers in collections from area A were about one-tenth of those from area B, and in August approximately equal in the 2 areas. The following May chalcids were about twice as numerous in the sprayed as in the check area.

Dryinidae

On sticky trap boards and by sweeping before treatment 8 Dryinidae were taken in area A and 13 in area B; after treatment 13 more were taken in B and only 2 in A, 2 days and 10 weeks after application.

Embolemidae

Several Embolemidae were swept from area A in August.

Pompilidae

Pilpomus sp. One nest found July 12 under a stone in a dry portion of area A contained three live larvae.

Priocnemus germanus (Cress.). This was a moderately common species in area A in mid-July, becoming abundant in August. It was taken in fly traps, by sweeping, and in general collecting. Survived.

Priocnemus conicus (Say). This species was common during May, but disappeared in both areas after treatment. The following May several specimens were seen in the treated area. Survived.

Formicidae

Aphaenogaster treatae Forel. Nineteen workers were found dead in trays in area A within 3 weeks after the spraying, none in area B. Molasses-trap collections, which were twice as abundant in area B as in A, showed that this species seemed greatly reduced by the spray, becoming more abundant 3 months later (table 9).

Camponotus (Myrmentoma) spp. Twenty-five specimens were taken in area A trays, one in area B. Scanty tree-jarring collections indicate that this species was eliminated (table 1).

Camponotus herculeanus pennsylvanicus (Deg.). Taken in numbers only in area B.

Crematogaster sp. Twenty-five specimens were taken in trays in area A within 8 days after the spraying; none in area B. In June greater numbers were taken by sweeping in area A than in B. Probably not affected.

Formica exsectoides Forel. Counts of ants taken on the domes of several nests before and after the spraying showed no detrimental effects of the spray. When these nests in area A were opened on July 12, pupae and many workers were found.

Formica fusca var. *subsericea* Say. Counts of ants about the entrances of 8 underground nests before the spraying ranged from a few to 65 specimens per square yard. Observations a few hours after the spraying showed no detrimental effect on the ants as they transported caterpillars killed by the poison to their nests. Counts of workers made periodically after the spray application were variable, but usually the numbers were as great as before the spraying. Although counts made July 12 were lower than pretreatment counts, when the nests were opened they contained many workers and brood. Two nests were abandoned, apparently from natural causes. A few specimens were taken by tree jarring and in molasses traps (tables 1 and 9). Not affected.

Formica neogagates Emery. Small numbers taken by sweeping indicated a greater abundance in area B than in A.

Formica pallide-fulva Latr. Several nests observed before the spraying were later abondoned, apparently from natural causes. One small colony under a stone contained many workers late in May, only 5 on June 16, but numerous ants again by July 12. Another colony was flourishing a week after the spraying. Not affected.

Lasius brevicornis Emery. Small colonies under stones were observed in May in a burned-over area on top of a ridge in area A. When looked at again on July 12 no colonies could be found, but they might have been driven elsewhere by the stones becoming too hot.

Lasius claviger (Roger). A colony located beneath a stone was deserted just before time of spraying, but became reoccupied by July 12.

Lasius niger (L.) vars. Several times more specimens were found dead in trays in area A than in B. Sweep collections in June averaged 100 to 200 specimens per

hour, being slightly more abundant in area B. Other collections were variable (tables 1 and 9). One nest with an abundant population was not affected by the spray and was full of workers and brood when last examined on July 12. Not affected.

Leptothorax curvispinosus Mayr. Not taken until late in June, being more abundant in area A than in B.

Leptothorax longispinosus Roger. Less abundant late in June in area A than in B, where they were swept at the rate of 600 specimens per hour. Not affected.

Myrmica spp. Two colonies observed one-half hour and a day after the spray application were apparently unaffected. Workers were observed carrying spray-killed leaf-roller larvae to nests.

Tapinoma sessile (Say). The comparatively small numbers taken in molasses traps (table 9) suggest that this species was reduced by the spray. Sweep collections for June, on the other hand, averaged 78 specimens per hour in area A as compared with 66 in area B. Probably not affected.

Foraging worker ants seemed well exposed to DDT, and it was interesting that after the first week they seemed little affected by the spray residue. Ants of several species were seen carrying spray-killed insects into their nests, but these insects seemed to have no effect on the strength of the colonies. Since affected insects dropped to the ground for weeks after the spraying, and since the number of aphids and the quantity of honeydew were increased as a result of the spray, the food supply of most species of ants remained plentiful throughout the season. Apparently this available food enabled the ants to replace easily those of their numbers killed by the insecticide.

Vespidae

Ancistrocerus tigris (Sauss.). A few males and females were collected in area A before the spraying in May and again during July and August. Survived.

Ancistrocerus spp. A few specimens collected in the treated area throughout the summer and during the following May were *A. tigris* (Sauss.) and *A. antilope* (Panz.), the former being more common.

Vespa crabro L. Fly-trap collections before treatment included 2 queens from area A and 10 queens from area B. After treatment this species was taken once in area A late in June, and four times in area B. Two other specimens were seen in the sprayed area, 1 day and 1 month after treatment.

Vespula spp. In the 2 weeks before treatment fly traps took 24 queens in area B and 3 from area A. In the 3 months after treatment 26 specimens were taken in area B and none in A. Seven queens were seen in area A a few hours after treatment, 2 of which appeared affected, making short flights and excitedly rubbing legs and mouthparts. Three more specimens were seen the next day, 1 of which seemed affected. One month after treatment 2 other normal specimens were seen. The species of *Vespula* collected were *arenaria* (F.), *maculata* (L.), *maculifrons* Roh., *rufa vidua* (Sauss.), and *rufa consobrina* (Sauss.).

Specimens of *Rygchium* and *Stenodynerus* were seen in the treated area in July and August.

Halictidae

Halictus spp. Several species were common on *Vaccinium* flowers at the time the spray was applied, and shortly afterwards a few bees were seen working as usual on the sprayed flowers. A day after the spraying two dead specimens were found in trays. Several specimens were seen in area A during July and August, and in the following May they were again common on *Vaccinium* spp. and *Gaylussacia* sp. Possibly slightly reduced; in normal numbers 1 year later.

Andrenidae

Andrena spp. Several species were common at the time of treatment, and were seen visiting *Vaccinium* flowers in a normal manner several hours after the plants were sprayed. One dying male was seen at this time. A few unaffected specimens were seen visiting *Vaccinium* 3 weeks later. Members of the genus were not collected again in either area the rest of the summer. The following May, 5 specimens were swept in area B, none in A. Probably reduced.

Bombidae

Bombus spp. Specimens were seen in small numbers in area A throughout the summer and the following May. Workers of *B. impatiens* Cress. were moderately common on flowers of *Melampyrum* (cow wheat) in mid-July. Probably unaffected.

Apidae

Apis mellifera L. Two similar-sized colonies of honeybees were brought in several weeks before the spray application. One was placed in the middle of area A and the other in unsprayed forest about 1½ miles distant. Both colonies were fed with sugar water prior to the spraying and before honey flow. The hive in area A was covered when this part of the forest was sprayed. Observations for several days after the spray application indicated that the bees were not affected by the poison while they were feeding on *Vaccinium vacillans* Kalm., the most abundant plant that was flowering late in May and early June. Bees did not appear to be affected when they drank water in a small pond in which most of the insect life had been destroyed by DDT. About 1 week after the spraying several hundred workers and a number of callow drone pupae were found dead near the entrance to the hive, whereas about 24 dead bees were observed near the check hive. At about this time the workers leaving and returning to the hive were few, probably because the field force had been decimated. Beginning about June 13 the colonies became very active and their pollen loads were noticeably heavier than before. On July 11, when both colonies were removed from the forest, they contained about an equal abundance of healthy workers.

ARACHNIDA

ARANEIDA

General collecting and observing of species in the study areas were the source of most of the data. A number of webs of several web-building species were located and tagged, and were visited before and after treatment. Four quadrats, each 7 feet square, were marked out in the study area to estimate the abundance of certain common species. Sweeping gave qualitative data and a rough idea of abundance of a large number of species. Specimens taken in sweeping ranged from 9 to over 400 per hour and averaged about 100. Spiders were collected also by tree jarring (table 1), in trays, and in Berlese funnels (table 10).

Of the 150 species collected in area A, some information as to the effect of the treatment was obtained for 64 species. These are discussed below.

Amaurobiidae

Amaurobius bennetti Blackw. This was one of the commonest species in area A throughout the summer, living under stones and bark. It was found in similar numbers 1 year after the treatment. Not reduced.

Titanoeca americana Em. This species was common under stones at the middle of area A throughout the summer. Immatures were seen in numbers the following May. Not reduced.

Dictynidae

Dictyna annulipes (Bl.) (=*muraria* Em.). This species lived in bark crevices of *Pinus rigida* Mill. and *Nyssa sylvatica* Marsh. Several trees, each with 10 or more spiders, were watched both years. Adults were found in June and July, immatures in August, and adults the following May. Not reduced.

Dictyna sublata (Hz.). This species was very common in area A prior to the treatment and was collected in large numbers by sweeping shrubs and herbs. Six specimens were found dead in trays the day following the treatment. Numbers were considerably reduced by DDT, but a few unaffected survivors were collected throughout the summer. The population was still low in area A, 1 year after treatment. Greatly reduced.

Theridiidae

Euryopis funebris (Hz.). Several immatures were taken by sweeping before the treatment and one 2 days later. Three males were collected in light traps and one female under bark 3 weeks after the spray application. Survived.

Theridion alabamense G. & A. Specimens were taken by tree jarring (table 1) and under bark scales of large white oaks in both areas throughout the summer. Probably not reduced.

Theridion frondeum Hz. This species was common in area A, where it was collected by sweeping and tree jarring. It was somewhat affected by the spray, but survived in numbers, possibly owing to its habit of often nesting in leaves spun together. One specimen was found dead in a tray 2 days after treatment. Numbers were still reduced to probably less than half pretreatment abundance 1 year after application. Moderately reduced.

Theridion kentuckyense Keys. Ten specimens were collected by tree jarring (table 1) in area A before the spray application and none after. Two affected specimens were seen 6 hours after treatment. Four specimens were found dead in trays 1 to 2 days after the spraying, one other after 8 days. Several specimens were taken in area B in May, June, August, and the following May. Greatly reduced or eliminated.

Theridion murarium Em. In area A, 21 specimens were taken by tree-jarring collections before the spraying (table 1), but no others until 3 months later, when 2 specimens were taken. Nine specimens were found dead in trays 1 to 2 days, and 5 between 3 and 14 days after the spraying. One unaffected specimen was swept 2 days after the spray application, another after 18 days. Immatures and adults were fairly common in area B throughout the summer. Greatly reduced.

Theridion unimaculatum Em. Five immatures were swept from the upper part of the sprayed area 6 days after treatment, one specimen was swept after 1 month, and another after 2½ months. Survived.

Erigonidae

Ceraticelus fissiceps (Camb.). Five specimens were swept from area A, two months, 4 specimens 2½ months, and 3 specimens 1 year after treatment. Several immatures, probably *C. fissiceps*, were swept 2, 6, and 18 days after spraying. Survived.

Linyphiidae

Lepthyphantes zebra (Em.). Quadrat counts a few days before treatment indicated 6 individuals per 100 square feet over several large sections of the treated area. No specimens were found in area A after treatment; the species was common throughout June and the following May in area B. Eliminated.

Linyphia maculata Em. Quadrat counts immediately before treatment showed about 6 subadults per 100 square feet over several extensive areas where *Vaccinium angustifolium* Ait. was the dominant ground cover. Four to 8 hours after the spraying a search revealed only two unaffected specimens and numerous deserted webs. No specimens were found a day after treatment or thereafter in area A. Adults were seen in unsprayed regions throughout June, and immatures were swept from area B in August and in the following May. Eliminated.

Linyphia marginata C. Koch. One specimen was collected by sweeping and 3 webs were tagged before treatment. The webs were deserted 8 hours after the spraying. The species was not taken again in area A, but was recovered in area B in June and August. Greatly reduced or eliminated.

Pityohyphantes phrygiana (C. Koch). Twenty-six females were located several days before treatment, and visited just before and after the spraying. Between 4 and 8 hours after the spray application only 2 were alive, 1 of which was affected; both were gone the next day. Two days after the spraying a search revealed no living specimens in about 30 additional webs. Adults continued to be common in unsprayed areas in June, immatures in August, and adults the following May, but specimens were absent from area A. Eliminated.

Argiopidae

Aranea spp. Immatures were common in area A before treatment and were seen in small numbers up to a month afterwards. Six specimens were found dead in trays 1 to 2 days following the spray application. Six deserted *Aranea* webs and one affected immature of *A. solitaria* (Em.) were seen 4 to 8 hours after the spraying. In July, August, and the following May no specimens were found in area A, although several were taken by sweeping and tree jarring in area B. Species collected were *A. raji* Scop., *foliata* (Four.), and *solitaria*, in the order of their abundance. Greatly reduced or possibly eliminated.

Araniella displicata (Hz.). Six specimens were taken by sweeping and tree jarring the week before the spraying. Five specimens were found dead in trays 1 to 2 days after treatment; not collected again in area A until August, when 4 small immatures were collected by sweeping. One immature was jarred from white oak the following May. A few adults were taken in area B in June, and immatures in August and the following May. Reduced.

Cyclosa conica (Pallas). Five of eight webs tagged just before treatment were empty 4 to 8 hours after the spraying, the 3 still occupied being on the margin

of the treated region. One day later these 3 webs were also deserted. One affected specimen was seen dangling on a partially completed orb 3 hours after treatment. The species was not taken again in area A, but was common in June, August, and the following May in surrounding unsprayed areas. Eliminated.

Leucauge venusta (Walck.). Six hours after the spraying, 2 of 3 webs that were occupied the previous day were empty, and the third contained an affected spider dangling from the orb. The day before the spray application 2 specimens were swept from area A, but no other specimens were collected there during the summer; 7 specimens were swept from area B in June. The following May, 4 immatures were seen on webs in area A, and 5 more were taken by sweeping. The species was thus reestablished in numbers not noticeably below pretreatment abundance. Whether this was due to survival or to repopulation from surrounding areas was not determined. Greatly reduced but reestablished a year later.

Tetragnatha versicolor Walck. (=*extensa* Seely). Five specimens were found dead in trays 1 to 2 days after treatment. A few immatures were collected by sweeping in June, August, and the following May. Survived.

Argiopid spiderlings. Several swarms of spiderlings (50-150 individuals each, probably *Aranea* spp.) were found emerging about the time area A was sprayed. Four apparently unaffected swarms were found 1 day after the spraying, the spiderlings being grouped around the egg sacs and obviously having just emerged. The next day those in 3 of the swarms were dead. In the fourth swarm about one-tenth of the original number were found dead, the remainder being either dispersed or taken by predation.

Three days after the spraying two more swarms were found. The following day all the spiderlings in one swarm were dead, whereas in the other about 5 percent were dead and the rest still active but dispersed. Five spiderlings were taken by sweeping in June, but none thereafter. Greatly reduced and after June possibly eliminated.

Agelenidae

Agelenopsis utahana (C. & I.). Immatures were very common over most of area A before the spraying, when there were roughly 2 webs per 100 square feet of forest floor. One day after the application 6 of 30 fresh webs were deserted. Three days afterward 12 of 20 webs were empty in area A, whereas in B, 15 webs were located, all of which were occupied. The species continued to be moderately abundant in area A throughout the summer, but was possibly about half as common as in area B. The following May it was still reduced in area A, there being considerably less than 1 web per 100 square feet of forest floor in several regions. Moderately reduced.

Cicurina spp. Specimens were collected in Berlese funnels and under stones in small numbers throughout the summer in both areas. Adults collected were *C. arcuata* Keys. and *C. brevis* Em. Probably not reduced.

Coras fidelis Bks. Common under bark and stones throughout the summer in both areas. Not reduced.

Wadotes calcaratus (Keys.). Collected with *Coras* in somewhat similar localities but in small numbers. Probably not reduced.

Pisauridae

Pisaurina mira (Walck.). This species was swept from cinnamon fern and other herbaceous undergrowth in fairly large numbers in areas A and B throughout the summer. Not reduced.

Lycosidae

Lycosa spp. These spiders were fairly common under stones and among dead leaves throughout the summer and the following May. Their numbers were difficult to estimate, but did not seem to change with the application of spray. Most of the adults collected were *gulosa* Walck., *frondicola* Em., and *pratensis* Em. in descending order of abundance. About 20 *L. gulosa* and *L. frondicola* females with eggs were seen 1 year after treatment. Not reduced.

Pardosa distincta Blackw. This species was common in hair grass (*Deschampsia*) near the middle of the treated area throughout the summer. Not reduced.

Pardosa xerampelina Keys. Specimens were locally common all summer along a small stream in area A. Not reduced.

Pirata maculatus Em. Adults were common in two microhabitats of area A in May, June, and the following May. Not reduced.

Pirata minuta Em. Several adults were collected in May and June along a small stream in the treated area. Survived.

Thomisidae

Coriarachne versicolor Keys. Small numbers were taken in area A throughout the summer by jarring white oak trees (table 1). Several other specimens were collected under bark scales on white oak and pitch pine. Not reduced.

Misumenops spp. From area A, 25 specimens were swept 2 weeks, 13 specimens 2 months, and 9 specimens 1 year after treatment; a comparable number were collected in the untreated area. *Misumenops* was common in dry sites (*Kalmia* and *Vaccinium* growth) throughout the summer. Adults taken were predominantly *M. celer* (Hz.), but also *M. asperatus* (Hz.) and *M. oblongus* (Keys.). Not reduced.

Philodromus pernix Blackw. This species was collected largely by tree jarring (table 1). One affected specimen was observed struggling at the base of a pine 4 hours after the spray application. Six specimens were found dead in trays after 1 to 2 days. Moderately reduced

Philodromus spp. (except *pernix*). Four specimens were found dead in trays 1 to 3 days, 3 others 5 days, and 1 other 15 days after treatment. Several unaffected specimens were swept from the treated area 2 days and 2 weeks after treatment. One specimen of *P. marxi* Keys. was collected 1½ months after the spraying, and two specimens of *P. rufus* Walck. were jarred from white oak 1 year after application. Adults collected were *P. rufus, P. marxi,* and *P. minutus* Bks. Survived.

Thanatus lycosoides Em. A few unaffected immatures were seen in grass near the middle of area A, 1½ and 3 months after the spray application. Survived.

Xysticus fraternus Bks. Immatures were swept in fairly large numbers throughout the summer. Fifteen specimens were taken 2 weeks, 18 specimens 1 month, and 30 specimens 2 to 3 months after treatment. A few specimens were also collected in area A the following May. Not reduced.

Gnaphosidae

Callilepis imbecilla (Keys.). Several specimens were

seen among dead leaves in both areas—adults in June and July, and immatures in August. Survived.

Drassodes neglectus Keys. Several specimens were found under stones in dry open parts of area A. Two females were observed with young on August 28. Survived.

Gnaphosa gigantea Keys. Adults were common under stones in dry parts of area A in May, and immatures in August. Survived.

Clubionidae

Clubiona spp. Taken in small numbers in both areas by tree jarring (table 1) and by sweeping throughout the summer, but were commoner in B. Two specimens were found dead in trays 1 day after treatment. Adults collected were *C. abboti* L. Koch, *C. obesa* Hz., and *C. pygmaea* Bks. Survived.

Phrurotimpus spp. Specimens were collected largely by turning stones or searching through dead leaves, but also in Berlese funnels. They were moderately common throughout the summer. Adults taken were mostly *P. palustris* Bks., but also *P. borealis* Em. Not reduced.

Salticidae

Habrocestum pulex (Hz.). This species was moderately common among rocks in several parts of the treated area throughout the summer and the following May. A few specimens were taken by sweeping and tree jarring 1 and 3 months after the spray application. One specimen was found dead in a tray 2 days after treatment. Survived.

Metaphidippus protervus (Walck.). Several specimens were taken by tree jarring and many by sweeping in area A before treatment. After treatment the population was depleted to possibly one-fifth of its former abundance, although still common in untreated areas throughout the summer. Fourteen specimens were found dead in trays 1 to 2 days after treatment. The population was still much below that in surrounding untreated areas 1 year after the spray application. Greatly reduced.

Phidippus sp. Forty-five immatures, probably *P. clarus* Keys., were swept from area A, 2 weeks after treatment. The species was equally common in area B during the same period. Five late immatures of *P. clarus* Keys. were taken in area A, 2 months after the spraying. Survived.

Zygoballus bettini Peck. Specimens were swept in small numbers from area A before the spray application, and several times during the following month. One specimen was taken the following May. Not collected in area B. Survived.

Several species were observed in numbers insufficient to indicate the effect of the treatment on them. The following species were taken between 3 weeks and 3 months after the spraying and apparently survived in the treated area: *Lathys foxii* Mx., *Scotolathys pallida* Mx., *Uloborus americanus* Walck., *Euryopis funebris* (Hz.), *Ulesanis americana* Em., *Theridion differens* Em., *T. globosum* Em., *Ctenium pumilus* (Em.), *Cornicularia pallida* Em., *Hypselistes florens* (Camb.), *Ceraticelus emertoni* (Camb.), *C. similis* (Bks.), *Ceratinopsis interpres* (Camb.), *Catabrithorax oxypaederotipus* (Cros.), *Neoscona arabesca* (Walck.), *Ozyptila* sp., *Anyphaena* sp., *Agroeca pratensis* Em., and *Castianeira cingulata* C. Koch.

An estimate of the effects of DDT was obtained for 31 species or species groups of spiders, whereas fragmentary information was acquired on 33 others. Of the 31 species, 7 were probably eliminated from the area (Group 1), 8 were moderately or greatly reduced (Group 2), and 16 were only slightly if at all affected (Group 3). The first group was composed entirely of web builders, species usually living out in the open and more or less exposed to the spray. In the second group the web builders also predominated, but forms like *Philodromus pernix* and *Metaphidippus protervus* that run over leaves and bark were also included. In the third group, among the species probably unaffected, were (a) those that live under loose bark, (b) those that live under stones, and (c) those that live among the dead leaves of the forest floor. Species of this last group obviously had little chance to contact the poison. The apparent immunity of the wolf spiders and other species active on the forest floor may be partly due to the fact that the leaf canopy allowed little DDT to settle on the ground. *Agelenopsis utahana* and *Lepthyphantes zebra*, both of which build webs near the ground, were affected, however.

It is interesting to note the degree to which the habits of individual species seem of importance in determining the extent of mortality. For example, *Theridion kentuckyense*, *T. frondeum*, *T. murarium*, and *T. alabamense* are all of approximately the same size and structure. *T. kentuckyense* nests up in the leaf canopy and was greatly reduced, or possibly eliminated, from the treated area. *T. murarium* nests largely among branches and bark crevices, and was severely depleted in numbers but not eliminated. *T. frondeum* nests both in the leaf canopy and in shrubs, often spinning leaves together above the web into a protective retreat. It was moderately reduced, and survived in considerable numbers. *T. alabamense* was taken only in small numbers, but there are indications that it was little if at all affected, probably owing to its habit of nesting under scales of loose bark. Similarly, a shrub and herb-inhabiting species of *Dictyna* was severely depleted in numbers by the spray, while another species living under bark scales of large trees was probably unaffected.

ACARINA

Paratetranychus ununguis (Jac.). This species was prevalent on the upper surface of *Quercus alba* and *Q. montana* leaves in both areas before the spraying. Although fully exposed to the spray, thriving populations of 10 to 20 individuals and 40 to 60 eggs per square inch of leaf surface occurred in August in a section of area A showing the heaviest deposit of DDT spray. The mites crawled over the DDT crystals in an unconcerned fashion and made feeding punctures adjacent to them. Chemical and biological tests, however, showed these crystals to contain little DDT at this time. On May 29, 1946, damage caused by these mites to red maple was particularly noticeable. Feeding by hundreds of individuals caused the foliage to be off-color and close examination showed fine stippling. The yellow areas were prominent, and where a number of the injuries had coalesced, the leaves were blotched. The discoloration was recognizable about 20 feet away. Counts of mites on leaves selected at random from different trees ranged from 30 to over 100 per leaf, and eggs were abundant too. A collection of leaves from trees in area B was made, but no

mites were found. The following August a careful search for this mite was made in area A, but none could be found, so probably the outbreak was over. At least 1 important mite predator, *Coniopteryx vicina*, was greatly reduced by the spray, and this in part may have accounted for the outbreak of mites.

Tetranychus atlanticus McG. This mite was abundant on *Aralia nudicaulis* L. in both areas after the spray application. It feeds on the undersides of the leaves and therefore was not exposed so directly to the DDT spray as was the previous species.

The general increase in tree-inhabiting mites in area A after the spray application was reflected in the tree-jarring data, although no attempt was made to pick up all the mites that fell on the sheets (table 1).

STUDIES IN AREA C

Description of Area C

This area is located near Maple Lake in Spring Brook Township, about 6 miles southeast of Scranton, Pa. It is an irregular-shaped 350-acre tract containing rather open stands of red maple, sugar maple, beech, and considerable overgrown swampy pasture and hemlock swamp. There is a heavy herbaceous undergrowth, including large areas of hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore), considerable laurel, and some rhododendron. Bowback Creek arises in and flows through the area.

Spray Application

On June 9, 1945, this area was sprayed with a DDT-oil solution from an N3N-3 biplane equipped with a multiple-nozzle distributing device. The formula used per gallon of spray was 1 pound of DDT, 1 quart of xylene, and 2.82 quarts of horticultural spray oil. This spray was applied at the rate of 1 pound of DDT per acre. The morning was calm, and hence ideal for applying the spray. No samples of spray deposits were taken for chemical analyses to ascertain the quantity of DDT reaching the ground.

Discussion

The terrestrial insects in area C were not studied intensively, because emphasis was placed upon the heavier DDT treatments on areas A and D. The lower part of Bowback Creek, which runs through area C, was studied in detail and information obtained on the effects of the spray on aquatic invertebrates has been published (Hoffmann *et al.* 7). Data on terrestrial forms were limited to those obtained from tray collections from June 9 to 27 and from 2 sweep collections made on June 8 and July 2.

Since the mayflies (mostly *Siphlonurus typicus* Eaton) and the stoneflies (mostly *Leuctra* sp.) naturally die and fall within a few days, their presence in the trays could not necessarily be attributed to the action of DDT. Excluding these orders (649 specimens), the remaining 537 specimens collected from the trays were mostly Diptera (47%), Lepidoptera (29%), Coleoptera (11%), and Hymenoptera (6%). Fifty-two percent of these dropped within 2 days and 85% within a week after the spraying.

Altogether 166 species or groups (determination to genus or family) found dead in the trays were tabulated. The more abundant ones will be discussed briefly. Eleven *Psylla annulata* nymphs were killed within 3 days after the spraying. Of the beetles, 23 *Cantharis* spp. and 7 *Luperodes meraca* succumbed shortly after the spraying. The spray was very effective against small caterpillars. Geometrids included 100 specimens of *Alsophila pometaria*, 13 *Phigalia titea*, and 17 that were not identified. Other caterpillars, mostly Phalaenidae, included 7 *Lithothane antennata* (Wlk.), 5 *Orthosia hibisci*, and 29 that were not identified. Fifteen small moths were also taken in the trays. The predominating dipterons killed and their numbers were as follows: 9 *Erioptera*, 25 *Hydrobaeninae*, 7 *Paratendipes albimanus* (Meig.), 9 *Palpomyia*, 40 *Lycoria*, and 31 *Hylemyia*.

A 1-hour sweep collection made about 3 weeks after the spraying yielded far more specimens than did a comparable sweep taken a day before the spraying, probably because the pretreatment collection was made too early in the season for an abundance of many species. Only the more numerous forms taken in the 2 sweeps will be considered here. Nymphs of *Lygus oblineatus* (Say) and adults of *Kleidocerus resedae* occurred in about equal numbers in both sweeps, as did also leafhoppers, such as *Erythroneura* spp. and *Empoasca* spp.. One cicadellid, *Agallia quadripunctata* (Prov.), may have been affected by the spray, for it was taken at the rate of 8 specimens per hour before and 1 per hour after the spraying. The aphid population remained about the same. Only 4 cantharids were taken before the spraying compared with 23 afterwards. One chrysomelid taken in numbers initially was not taken later. Lepidopterous larvae on herbage and shrubs were twice as abundant after treatment (32 per hour) as before, and small moths were abundant (86 per hour) only in the posttreatment collection.

Tipulidae were taken in both sweep collections, but the species in each were largely different. Tendipedids were abundant 3 weeks after the spraying, the Hydrobaeninae averaging 337 specimens per hour after treatment, three times more than initially; *Polypedilum* spp. and others were taken in small numbers both times. Members of the Heleidae occurred in equal numbers, and two times more *Lycoria* and about three times more Fungivoridae were taken after the spraying. Specimens of Dolichopodidae averaged over 100 per hour of sweeping before the spraying and twice this number later; several species of Empididae were more abundant later, while phorids occurred in equal numbers. Only 2 syrphids were swept before the spraying, compared with 21 of *Xanthogramma flavipes* later. Muscids were eight times more abundant in the later sweep, whereas a species of *Sapromyza* was slightly less abundant. Two adult *Drosophila* were taken per hour before the spraying compared with 282 later, while collections for Sepsidae were 3 and 81, respectively.

Fifty-two sawfly larvae were taken in the first sweep but none later. Braconid parasites were a third more abundant after the spraying. Of the

ichneumonids, *Orthocentrus pusillus* occurred in equal numbers, whereas 12 specimens per hour of *Eusterinx compressa* were swept before treatment compared with 1 afterwards; other species occurred in small numbers both times. Diapriids occurred in similar numbers after the spraying, whereas there were 2½ times more chalcids. Ants, such as *Formica fusca* var. *subsericea, Lasius niger* (L.) vars., *Leptothorax longispinosus, Leptothorax curvispinosus, Myrmica* spp., and *Tapinoma sessile,* were all scarce before the spraying but very abundant 3 weeks later.

A variety of spiders were collected, but not many individuals of each species. Nine *Dictyna* sp. were swept per hour before the spraying and only 3 afterwards, whereas collections for *Theridion frondeum* were 4 and 2, respectively. About 11 each of Linyphiids and of Argiopids were taken in each collection. The thomisids, *Misumenops* sp. and *Xysticus* sp., were slightly more abundant after the spraying. Phalangida, which are quite susceptible to DDT poisoning, were captured in equal numbers in both sweeps (6 per hour).

A brief survey of area C following its treatment at the rate of 1 pound of DDT per acre indicated that the toxicant was very lethal to many species of lepidopterous larvae, including 2 forest pests. Psyllids, small moths, and several genera of small flies were killed in numbers shortly after the spray was applied. A sweep collection made 3 weeks after the spray application compared with one made the day before the spraying showed that practically all groups of insects were as abundant or more so afterwards. Many species were taken in the later sweep for the first time.

STUDIES IN AREAS D AND E

Description of Area D

This tract is located within the Patuxent Research Refuge, Bowie, Md. It includes 117 acres of deciduous moist bottomland forest and a section of the Patuxent River. The trees are mostly large and form a closed canopy. The principal tree species include tulip poplar (*Liriodendron tulipifera* L.), beech (*Fagus grandifolia* Ehrh.), river birch (*Betula nigra* L.), American hornbeam (*Carpinus caroliniana* Walt.), sweet gum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica* Marsh.), American elm (*Ulmus americana* L.), and white oak (*Quercus alba* L.). Poison ivy (*Toxicodendron radicans* (L.)) growth is luxuriant. The dominant herbaceous plants include wood nettle (*Laportea canadensis* (L.) Gaud.), touch-me-not (*Impatiens biflora* Walt.), jack-in-the-pulpit (*Arisaema triphyllum* (L.) Torr.), springbeauty (*Claytonia virginica* L.), mayapple (*Podophyllum peltatum* L.), and the cutleaf coneflower (*Rudbeckia laciniata* L.). Although the land drains well, heavy rains in the summer cause much of it to remain wet, and a part of the area is often inundated. Exceptionally heavy rains about the middle of July 1945 caused flood waters to cover the study area with from 1 to 3 feet of water. This destroyed so much of the fauna that studies were discontinued.

Description of Area E

About 1 mile up the Patuxent River from area D is a similar section of forested land that served as a control area. It was somewhat higher and appeared to have a more luxuriant growth of wood nettle and touch-me-not. Though the two areas were similar, insect collections showed area E to have the more abundant fauna.

Spray Application

Area D was sprayed between 7 and 9 p.m. on June 5 with a DDT-oil solution by an N3N-3 biplane fitted with a multiple-nozzle distributing apparatus beneath the wings. The formula per gallon of spray was 1 pound of DDT, 1 quart of xylene, and 2.65 quarts of No. 2 fuel oil. It was applied at the rate of 2 pounds of DDT per acre. There was a brisk breeze at first (wind velocity about 6 miles per hour), and some of the spray drifted more than one-fourth mile from the point of application. A search was made for DDT crystals on the foliage of the lower branches of trees and other vegetation, and infrequently a few patches of fine crystals were found, but along a road bounding one side of the sprayed plot, in places not overhung by trees, many patches of crystals could be seen easily on low foliage. Eighteen Petri plates 4 inches in diameter exposed in somewhat open sites along the river banks averaged 0.6 pound of DDT per acre, range 0.004 to 1.44. Another set of 18 plates exposed on open forest floor beneath the tree canopy gave an average analysis of 0.05 pound of DDT per acre, range 0.002 to 0.21, whereas the deposit on 42 similar plates under the tree canopy and also beneath shrubs and lower vegetation averaged only 0.008 pound per acre, range 0.0008 to 0.06. Because the forest canopy is dense, it is assumed that a much higher dosage was deposited on the treetop foliage.

Discussion

Typical of all DDT sprayings, many insects were killed within a few hours after the spray application. The effect of the DDT applied at the rate of 2 pounds per acre was not prolonged, however, and most of the species studied were present in considerable numbers 2 or 3 weeks later (tables 11 and 14). The area treated was fairly small, so the possibility of species immigrating into it from untreated forests was greater than in area A.

Moths were reduced by about 70%, a week after the spraying as compared with pretreatment catches, but by the end of 3 weeks the populations in the sprayed and check areas were almost equal. Two species of geometrids were reduced in numbers. Scanty collections indicated that tree-inhabiting caterpillars were decimated. The Hymenoptera were tabulated as a group, and, although greatly reduced immediately after the spraying, the population was equal to that of the check area 1 month later. The large numbers of Diptera taken on sticky trap boards

and in light traps showed no reduction in the sprayed area. On the other hand, considerable data on Calypterate flies captured in fly traps indicated an overall reduction in their numbers of about 85% for about 2 months. Many of the leaf-feeding beetles were also greatly reduced in numbers.

The abundance of honeydew on understory trees and plants, coupled with a study of aphid colonies developing on some of this growth, showed that they were not reduced by the spray and probably increased in numbers. Most of their parasites and predators appeared to be unaffected.

Ground forms, including carabids, silphids, and staphylinids, were relatively unaffected by the spray, although certain species with an emergence peak at that time were moderately reduced. Data on ants suggested that they were initially reduced in numbers, but not affected by the residual spray a week later. Arachnids maintained their populations with the exception of *Leiobunum*, which was practically eliminated. This phlangiid crawls around over foliage and consequently probably came in contact with many DDT crystals.

ANNOTATED LIST OF INVERTEBRATES STUDIED IN AREAS D AND E

Insecta

Collembola

Springtails caught in molasses traps a week after the spraying showed that they were not adversely affected by the poison (table 16).

Orthoptera

Blattidae

Parcoblatta sp. Collected in area D only, more abundantly a week after than a week before the spraying (table 16).

Gryllacrididae

Ceuthophilus sp. Their numbers were not reduced by the spray (table 16).

Tettigoniidae

Amblycorypha sp. Small numbers of nymphs were swept in both areas before and after the spraying.

Scudderia sp. Nymphs became abundant in both areas 3 weeks after the spray application.

Tettigidae

Tettigidea lateralis Harr. A few were collected by sweeping, most of them in area D on June 14 and 22.

Odonata

Agrionidae

Agrion maculatum Beauv. Teneral specimens, mostly males, were moderately common and widely distributed in both areas before treatment. Observations of June 21 showed no diminution in numbers in either area.

Hemiptera

Pentatomidae

A few specimens of 5 species were taken in area D, 2 days after the spraying.

Nabidae

Nabis sordidus Reut. Eight specimens per hour were collected by sweeping in area D, 2 days after the spraying, after which nymphs and adults were always more abundant in area D than in E. Not affected.

Miridae

Several mirids were common in area E, but none occurred in important numbers in area D before or after treatment.

Cercopidae

Aphrophora quadrinotata Say. Six specimens per hour were swept in area D a week after the spraying, and 2 per hour in area E.

Cicadellidae

Agallia quadripunctata (Prov.). Sweep collections in both areas averaged about 10 specimens per hour before the spraying and smaller numbers afterwards. Not affected.

Balclutha impicta (VanD.). Not abundant until early July, when it was 3 times more abundant in area D than in E.

Gypona octolineata (Say). Seven specimens per hour were collected in both areas late in June.

Two days after the spraying a variety of cicadellid nymphs occurred in small but approximately equal numbers in both areas.

Fulgoroidea

Scattered specimens of several species were taken in both areas 2 days after treatment. Early in July the numbers in collections increased considerably.

Aphidae

Amphorophora vaccinii Mason. Twenty-two per hour were taken by sweeping in area D on June 22.

Anuraphis sambucifoliae (Fitch). A colony of 150 of these aphids and perhaps 50 associated ants, *Camponotus herculeanus pennsylvanicus* (Degeer), were first observed a few hours before area D was sprayed. Within 2 weeks the aphid colony had increased to 500 individuals.

Aphis heraclella Davis. Several colonies of from 30 to 100 individuals were located on *Cryptotaenia canadensis* (L.) DC. plants in both areas a few days before area D was sprayed. Ants, *Prenolepis imparis* (Say), were associated with each colony. In area D no change in populations was noted until about a week after the spray application, when some colonies were destroyed by syrphid predators and others by a hard rain.

Calaphis betulaecolens (Fitch). This species was taken by sweeping on June 1 and 22 in area D, and on July 4 in area E.

Cinara carolina Tissot. Two colonies, 1 of a female and 6 young and another of about 100 aphids, were found feeding on *Pinus virginiana* Mill. in area D the afternoon before it was sprayed. There was no apparent change in the colonies up to a week later. Both were accompanied by numerous herding ants, *Dolichoderus mariae* Forel.

Eriosoma lanigerum (Hausm.). Many well-infested curled leaves were marked for observation before area D was sprayed. Frequent observations up to a week after the spraying indicated no change in numbers attributable to the spraying. The leaves were tightly curled, and it is unlikely that much spray reached the aphids. Later the aphid populations on some leaves were decimated by syrphid larvae, *Metasyrphus vinelandi* (Curran).

Macrosiphum sp. In area D sweepings netted 9 specimens per hour on May 30, 68 on June 9, 223 on June 14, and 6 on July 2. In area E, 6 per hour were swept on July 4 only.

Macrosiphum rudbeckiae (Fitch). This aphid was abundant on *Rudbeckia laciniata* L. The aphids per colony in 12 colonies in area D and 10 in area E ranged from 30 to 1,300. Counts were made a few hours before the spray application and every other day thereafter for 2 weeks. Many of the colonies in both areas were greatly reduced by syrphid larvae, *Metasyrphus emarginatus* (Say), or by heavy rains on June 9 and 10. Some individuals became parasitized by Hymenoptera. Although most colonies were reduced from pretreatment numbers as a result of biological and climatic control, several maintained their original numbers or became larger. None of the colonies were adversely affected by the DDT spray. By June 20, females with young were found on additional plants throughout the sprayed area.

Macrosiphum ruralis H. & F. When first observed a colony in area D was comprised of about 45 adults and many young. Three days after the spraying the numbers had diminished considerably, probably as a result of predators, for a mirid nymph and 2 syrphid larvae were seen feeding on individual aphids. Three days later the syrphid larvae had increased greatly in size and a cantharid was taking a toll. A few days after this several alate females of this species were seen on adjacent plants and by June 23 many young had made their appearance there.

Observations on aphids living near the ground showed clearly that they were not disturbed by the application of the 2-pound DDT dosage. The abundance of honeydew on understory trees and plants suggested that species inhabiting trees were not reduced in numbers by the spray, and that there was probably an increase in the general population. This was indicated also by sweeping and sticky-trap-board (table 14) collections.

COLEOPTERA

Carabidae

Chlaenius aestivus Say. Scanty molasses-trap collections suggest that this species was greatly reduced (table 16).

Euferonia lachrymosa (Newn.). Occurred in equal numbers in both areas 1 week after the spraying (table 16).

Lebia lobulata Lec. One specimen was swept before treatment and 4 about a week later, in area D only.

Silphidae

Fish-trap collections made before the spraying and 1 week afterwards furnished data on this family (table 15).

Nicrophorus orbicollis (Say). This species appeared greatly reduced by the spray.

The numbers of *Nicrophorus tomentosus* (Web.), *Prinochaeta opaca* (Say), *Silpha inaequalis* (F.), and *Silpha noveboracensis* (Forst.) were not affected, possibly because their peak emergence was not reached until after the spray application.

Staphylinidae

Small numbers of several species of staphylinids were found dead in trays up to 2 weeks after the spraying. Most species taken in ground traps baited with fish were more abundant a week after than before treatment, and none appeared to be diminished by the DDT spray (table 15). The species taken included *Ontholestes cingulatus* (Grav.), *Philonthus cyanipennis* (F.), *Staphylinus maculosus* Grav., and *Tachinus fimbriatus* Grav.

Histeridae

Hister spp. These were collected in small numbers a week after the spraying and probably were not affected (table 15).

Lampyridae

A few specimens of *Ellychnia corrusca* (L.) were found dead in trays. Sweep collections made a week after the spraying averaged 4 times more specimens in area D than in E. Sticky-trap-board collections (table 14) also indicated that the peak population of lampyrids occurred after the time of the spray application and that the spray caused no important losses.

Cantharidae

Cantharis flavipes Lec. Eighteen adults were found dead in trays in area D, 1 day after the spraying. A week after the spraying the species was more numerous in sweep collections from area D than from area E.

Cantharis umbrinus Green. Within 3 days after the spraying 28 specimens were found dead in trays in area D compared with 3 in area E; scattered specimens were in the trays of area D throughout June. In area D sweep collections totaled 24 per hour on May 30, 1 on June 9, 136 on June 14, 58 on June 22, and 138 on July 2, whereas in area E they totaled 34 on June 7, 46 on June 12, 4 on June 25, and 10 on July 4. About 2 weeks after the spraying 77 beetles were taken in 10 box area samples in area D compared with 8 from an equal number of samples in area E. Initially reduced, but later increased to an abundance greater than that in the check area.

Podabrus rugosulus Lec. This species was downed by the spray as indicated by 12 specimens in trays the day after the application. In sweep collections it was most abundant before the spraying in area E, equal in the 2 areas a week after treatment (40 specimens per hour), and afterwards was abundant in area D only. In box area samples the species was taken in about equal numbers from both areas 2 weeks after the spraying.

Sticky-trap-board collections of cantharids in area D showed a 70% reduction 1 week after the spraying, no apparent reduction 3 weeks later, and an increase a month after the spray application (table 14). All data point to an initial reduction in numbers due to the spray, followed by an increase exceeding the numbers in the pretreatment collections and those in the check area. This increase coincided with the increase in their aphid prey in the sprayed area.

Mordellidae

Scattered specimens of *Mordellistena* spp. were taken in trays in area D in June and early July. Sweep collections did not contain many specimens near spray time, but several species, especially *M. pubescens* (F.), became more abundant late in June and early in July, particularly in area E. Small sticky-trap-board collections indicated that this family was affected by the spray, but 1 month later numbers were again about equal in both areas.

Pedilidae

Pedilus newmani (Lec.). Small numbers were taken in both areas before the spraying but none afterwards.

Aderidae and Anthicidae

Within a week after the spraying 8 adults of *Zonantes fasciatus* (Melsh.) and 5 of the anthicid, *Notoxus murinipennis* (Lec.) were found dead in trays in area D.

Elateridae

Small numbers of several species were taken in trays in area D and by sweeping in both areas, both before and after spraying. Sticky-trap-board collections showed no significant reduction in numbers attributable to the spray (table 14).

Buprestidae

A few specimens, mostly *Agrilus subcinctus* Gory, were found dead in the trays a few days after the spraying.

Cyphonidae

Cyphon obscurus Guer. About 60 specimens were found dead in the trays within a week after the spraying, two-thirds of them the day after treatment. Sweep collections though meager indicated that this species was reduced by the spray.

Ptilodactylidae

Ptilodactyla serricollis (Say). Fifty-five adults were found dead in trays during June and July in area D, compared with 7 in area E.

The two preceding species were the major ones of the coleoptera represented in the sticky-trap-board collections (table 14), which showed that these families were reduced at least 80% by the spray.

Byturidae

Byturus unicolor Say. Small numbers were swept in both areas before and after the spraying. Apparently this species was not affected.

Coccinellidae

Adults were not common in either area. They were most numerous late in June. From July 2 to 14, 12 larvae were taken in the area D trays. Adult numbers apparently were not affected a week after the spraying, but later than that were not so abundant in area D as in E (table 14). On July 4, 28 larvae per hour were swept in area D, compared with 2 per hour in area E. This increase of larvae in area D was probably attributable to the large aphid population.

Alleculidae

Seven adults of *Hymenorus* sp. were found dead in the trays in area D within 3 days after the spraying.

Melandryidae

Symphora sp. Forty-three adults were found dead in the trays in area D within 3 days after the spraying, compared with 4 adults taken in the trays of the same area 3 days before treatment, and with none in area E.

Scarabaeidae

A few specimens of several genera were found dead in trays within a few days after the spray application. *Onthophagus hecate* (Panz.) and *O. janus* (Panz.) occurred in fish traps in area D only, a week after the spraying (table 15). Twelve adults of *Popillia japonica* Newm. were taken in area D trays between July 4 and 14, the residual poison apparently being enough to affect them at that time. Only 1 Japanese beetle was collected in the control trays.

Cerambycidae

A few specimens of *Oberea bimaculata* (Oliv.) were swept in area D on July 2. An occasional dead cerambycid was found in the trays of area D shortly after the spray application.

Chrysomelidae

The variety and numbers of beetles in this family found in the trays of area D for 2 weeks after the spray application attest that they were greatly affected by the spray. The most abundant forms found dead in the trays were *Diabrotica undecimpunctata howardi* Barber and *Orthaltica copalina* (F.). A month after the spraying both species were swept in equal numbers in areas D and E. A variety of other chrysomelids were taken by sweeping in both areas, but their numbers were not great enough to permit an individual evaluation of the effect of the DDT. Sticky-trap-board collections (table 14) show that the family as a whole was greatly reduced.

Curculionidae

The most prevalent weevils found dead in trays in area D within 3 days after the spray application were *Apion walshii* Smith, *Anthonomus scutellatus* Gyll., and *Eugnamptus* sp. A great variety of species were taken in small but approximately equal numbers in both areas at intervals after the spraying.

Scolytidae

Pseudopityophthorus minutissimus (Zimm.). Four specimens were found dead in the trays in area D.

MECOPTERA

Specimens of *Panorpa maculosa* Hagen and *P. venosa* Westw. were common in both areas before the spraying but almost absent in area D afterwards. *Bittacus strigosus* Hagen averaged 7 specimens per hour in sweepings made in both areas beginning June 22. Teneral specimens of this species were first collected a few days earlier. The time of emergence of this species with reference to the spray is probably the reason it was not affected.

TRICHOPTERA

Meager light-trap collections suggest that this order was moderately reduced in numbers for a week after the spraying and not affected much beyond that time (table 11).

LEPIDOPTERA

Data on adults were obtained from light traps and on larvae from sweeping and general observations.

Limacodidae

Lithacodes fasciola (H-S.). After the spraying adults were present in about equal numbers in both areas.

Citheroniidae

Anisota rubicunda (F.). A group of 6 small larvae were observed feeding on the underside of a red maple leaf a few hours before the forest was sprayed. When the colony was observed again 17 hours after spraying 5 of the larvae were dead and the other was noticeably affected by DDT. One adult was taken

at light in area D, 2 days and 3 additional ones 8 days after the spraying.

Lasiocampidae

Malacosoma americana (F.). Adults were not reduced by the DDT spray (table 12).

Geometridae

Adults of 2 species, *Heterophleps triguttaria* H-S. and *Ectropis crespuscularia* (Schiff.), apparently were greatly reduced in numbers by the spray, whereas the numbers of *Xanthorhoe lacustrata* (Gn.) were only slightly reduced (table 12). Other geometrids were taken in numbers too small for evaluation. Specimens of *Tetracis crocallata* Gn. were rather common in area D during June.

Phalaenidae

Lacinipolia renigera (Steph.). Adults were not reduced by the spray (table 12).

Stiriodes obtusa (H-S.). Occurred occasionally in both areas late in June.

Arctiidae

Halisidota tessellaris (A. & S.). Adults common in both areas late in June and early in July.

Light-trap collections showed a reduction of about 70% in the adult larger moths in area D a week after the spraying compared with pretreatment catches (table 11). The effect of the poison wore off and by the end of 3 weeks there was no apparent difference in the populations of both areas. A similar trend was shown by the sticky-trap-board collections (table 14). Most of the reduction noted was in 2 abundant geometrids. Most other species seemed unaffected (table 12). Sweep collections of small moths indicated approximately equal populations in the 2 areas both before and after the spraying. Tree-inhabiting caterpillars were evidently greatly reduced by the spray, for 20 dead larvae were collected in trays during the first 2 days after treatment in area D, compared with 1 in area E.

DIPTERA

Information on flies was obtained chiefly by sweeping, on sticky trap boards (table 14), and in fly traps (table 13), and light traps (table 11). Practically all data on Calypteratae (Muscidae, Sarcophagidae, and Anthomyiidae) were from fly-trap catches.

Tipulidae

Dolichopeza carolus Alex. Common and widely distributed in area D before the spraying, whereas only a few specimens were found there afterwards.

Epiphragma fascipennis (Say). Fairly common in swampy places in area D before the spraying, but none were seen afterwards.

Epiphragma solatrix (O. S.). Abundant in rank vegetation in the drier parts of the bottom land in area D before the spraying, compared with a few specimens taken 2 weeks after treatment.

Hexatoma wilsonii (O. S.). This species was abundant on rank vegetation bordering swampy places both before and after the spraying.

Limonia gladiator (O. S.). Sweep collections in area D averaged about 3 specimens per hour both before and after the spraying.

Limonia tristigma (O. S.). Sweep collections averaged 10 specimens per hour in area D about 2 weeks after the spraying, compared with 2 for area E. This species was not collected before June 14.

Pales macrocerus (Say). Occurred in small but equal numbers in both areas after treatment.

Tipula submaculata Lw. Common and widely distributed just before the spraying time throughout the bottom land, where it occurred at the rate of about 1 specimen per 400 square feet. Two weeks later only a few adults were taken in both areas.

Tipula triplex Wlk. Abundant in both areas 3 days before and 2 weeks after the spray application.

Members of this family emerged at different times. When the emergence period coincided with the time of the spray application, the species were reduced in numbers. Some species, such as *Liogma nodicornis* (O. S.), *Dicranoptycha sobrina* O. S., *Austrolimnophila toxoneura* (O. S.), and *Tipula submaculata* Lw., apparently had completed emergence before spray time, and though abundant just before, were not present in collections from either area after the spraying. Others, like *Pseudolimnophila* sp., *Brachypremna dispellens* (Wlk.), and *Limonia triocellata* (O. S.), did not emerge until later and were not affected by the spray.

Culicidae

Mosquitoes, mostly *Aedes canadensis* (Theob.), were found at the rate of about 1 specimen per square yard in both areas before the spraying. For a few days after the spraying no mosquitoes were encountered in area D. On June 12, one was occasionally bitten in area D and on June 14 mosquitoes were annoying, but most of the men working in the area did not bother to use repellents. The heavy population of mosquitoes in area E, on the other hand, caused the men to rely on repellents in order to work satisfactorily. About a week after the spraying mosquitoes were moderately abundant in area D.

Tendipedidae

Adults of *Cricotopus varipes* (Coq.), *Tanytarsus obediens* Joh., and *Tendipes decorus* (Joh.) were common in area D just before but apparently absent 2 weeks after the spraying. A few specimens of *T. decorus* were taken again early in July, but most of the tendipedids present on this date were different species from those observed before the spraying. Apparently members of this family were greatly reduced by the treatment.

Heleidae

Scattered specimens belonging to several genera were taken shortly after the spraying in area E, but only an occasional one in area D.

Fungivoridae

Specimens of 12 genera were taken by sweeping, but in insufficient numbers for drawing conclusions. Specimens from other collections were identified only to family, and these showed a reduction in numbers for at least 2 weeks after the spraying.

Lycoriidae

Sweep collections ranged from 0 to 114 specimens per hour, the larger numbers usually being from area E. These flies were scarce in both areas during the week following the spraying.

Itonididae

Small numbers were taken in area D after the spray application, but none in area E until early July.

Tabanidae

Species of *Chrysops*, particularly *C. wiedemanni* Krb., which were abundant and annoying just before the spraying of area D, were not evident there afterwards until about June 21, when they attained pretreatment abundance again.

Rhagionidae

Chrysopilus thoracicus (F.) and *Rhagio plumbeus* (Say) were common in area D before the spraying, but were not taken afterwards. *Chrysopilus quadratus* (Say), on the other hand, was moderately common both before the spraying and 2 weeks later.

Asilidae

Two unidentified asilids that were rather common in area D before the spraying were not taken afterwards.

Dolichopodidae

Sweeping collections ranged from a few to 450 specimens per hour. There was a great reduction in numbers in area D immediately after the spraying, but within 2 weeks the populations in areas D and E were similar.

Empididae

Several species taken immediately before the spraying were not taken in either area afterwards.

Phoridae

Box area samples taken 2 weeks after treatment showed that *Borophaga femorata* (Meig.) averaged 7 specimens per collection in both areas, whereas a species of *Megaselia* was considerably more abundant in the check area. Other species were swept in numbers before spraying in both areas, but the populations remained low until early July, when they averaged 28 per hour in area D and 98 in area E.

Syrphidae

Although collected in small numbers, adults and larvae were consistently more abundant in area D than in E, probably because of the abundance of aphid hosts.

Muscidae

Muscina assimilis (Fall.). The numbers in collections were reduced about 75% during the first 6 days after the spraying, and although the species increased in numbers from the seventh day on, was probably reduced in some degree through June and July.

Pyrellia cyanicolor (Ztet.). This species was reduced on an average 75% during the 2 weeks following the spraying (table 13), but was taken in large numbers in the treated area on the tenth day. After June 19 it was taken only occasionally in fly traps in both areas. Sweep collections showed a marked drop in population following the spraying but repopulation 2 weeks later. Moderately reduced.

Sarcophagidae

Sarcophaga spp. Daily catches in the treated area averaged 13 specimens before the spraying and 7 afterwards, although 80 were taken in the sprayed area on the tenth day after treatment. On an average about 75% of the species of *Sarcophaga* taken were *ventricosa* Wulp and 25% an undetermined species. Slightly reduced.

Anthomyiidae

Fannia canicularis (L.). In area D about 75 specimens were taken in the 8 days before the spraying and only 9 in the 4 weeks following. During the same periods in the untreated area about 50 were taken before and 40 after the spraying. Reduced.

Fannia fuscula (Fall.). About 80 specimens were taken in area D the week before treatment and only 1 afterwards, on June 17. The species was taken in small numbers in area E in June and July. Reduced.

Fannia sp. (*pusio* group). In area D about 80 specimens were taken the week before, and 25 specimens during the 8 weeks after the spray application. In area E about 60 specimens were taken before the spraying and 40 specimens afterwards. Slightly reduced.

Hebecnema vespertina (Fall.). About 150 specimens were taken in area D the week before the spraying. After treatment 1 specimen was taken June 8 and 4 specimens June 19. In area E, 90 specimens were taken before and 60 specimens after the spraying. Reduced.

Helina troene (Wlk.). About 40 specimens were taken in area D from May 30 to June 5. None were taken after the spraying. In area E about 75 specimens were taken June 1 to 4 and about 25 specimens June 11 to 26. Reduced.

Hylemya cilicrura (Rond.). During the week before treatment about 50 specimens were taken in area D and 150 in area E. In the 3 weeks following, 10 were taken in the sprayed area and 30 in the check area. Probably not reduced.

Mydaea spp. Numbers were reduced about 92% during the 8 weeks after the spraying (table 13). Specimens were taken in considerable numbers before the treatment and in the check area through June and July. Of the species taken about 60% were *M. ancilla* (Meig.) and 40% undetermined. *Mydaea ancilla* tabulated separately showed about an 85% reduction over the same period. Greatly reduced.

Pegomya connexa Stein. In the treated area 50 specimens were taken the week before the spraying and only 2 afterwards, on June 22 and July 3. In the untreated area 15 were taken before and 200 after the spraying, from June 6 to July 12. Greatly reduced.

Pegomya lipsia (Wlk.). This species was reduced by more than 95% during the 4 weeks after the spraying (table 13), but was collected only occasionally in July in either area. Greatly reduced.

Phaenicia caeruleiviridis (Macq.). Rather irregular data showed this species to be reduced an average of 91% for the 3 weeks after the spraying (table 13), although 20 specimens were taken in the sprayed area 7 to 10 days after treatment. Reduced.

Phaonia pulvillata (Stein). About 60 specimens a day were taken in area E through June and July. Data from area D were erratic, but indicate that the species was probably reduced during the 3 weeks after the spraying.

Phormia regina (Meig.). About 200 specimens were collected in area D during the 8 days before the spraying, and only about 80 specimens during the 4 weeks following. In area E, 40 were collected before and about 100 in the 4 weeks after treatment. Moderately reduced.

Platycoenosia mikii Strobl. This species was reduced about 80% in the 3 weeks after the spraying (table 13). It was not taken in July. Reduced.

Several calypterates were taken in small or irregular numbers, so that no estimate of the effect of treatment

on them could be made. The following were collected in area D within 8 weeks after spray application: *Calliphora* sp., *C. vicina* R. D., *Cynomyopsis cadaverina* (R. D.), *Pollenia rudis* (F.), *Anthomyia pluvialis* (L.), *Coelomyia subpellucens* (Ztt.), *Eustalomyia* sp., *Fannia scalaris* (F.), *Helina rufitibia* (St.), *Hydrotaea dentipes* (F.), *Limnophora arcuata* St., and *Myospila meditabunda* (F.).

Fly-trap collections indicate that the calypterate population as a whole was reduced about 85% by the spray application. None of the 10 most numerous species, however, were eliminated from the area treated for more than 4 days after the spraying. In the treated area catches remained low through June and July, and there were no signs of a gradual reestablishment of affected species. In the check area collections decreased during June, and through July averaged only slightly larger than catches from the treated area. This reduction may have been due to a decrease in bait attraction rather than to an actual falling off of the population.

Five species were collected in numbers large enough to indicate roughly their percentage of mortality (table 13). Six other species—*Muscina assimilis, Fannia canicularis, Hebecnema vespertina, Helina troene, Pegomya connexa,* and *Phormia regina*—were reduced by the spray, but were not taken in numbers large enough to be useful as quantitative data. Two other forms—*Sarcophaga* spp. and *Phaonia pulvillata*—were probably also affected. Evidence from a small amount of data indicates that *Hylemya cilicrura* was probably not affected. None of the calypterates taken in large numbers, however, showed immunity to the treatment.

Sphaeroceratidae

Data on *Leptocera* spp. based on sweepings and box area samples were erratic, probably indicating that numbers were taken only when a restricted habitat was sampled. Two weeks after the spraying these species were fairly abundant in area D.

Lauxaniidae

The species *Homoneura philadelphica* (Macq.) was taken in consistently greater numbers in area D than in E, both before and after the spraying. A species of *Pseudogriphoneura* did not appear in the areas until after the time of spraying. It was abundant late in June and early in July. Several species of *Sapromyza* were swept at the rate of about 10 specimens per hour in both areas before the spraying. Apparently these forms were almost eliminated, for afterwards only a few specimens were found in area D, whereas half of the pretreatment numbers were collected in the check area.

Chloropidae

This family was abundant in area E before the spraying but scarce in D. Sweepings made 3 weeks after the spraying averaged 5 specimens per hour in both areas. Two weeks after the spraying *Hippelates* was very annoying in area D but apparently less numerous in area E. Not affected.

Drosophilidae

Box-area-trap and sweeping samples indicated that members of this family, mostly *Chymomyza amoena* (Loew) and *Drosophila inversa* Walker, were not diminished in numbers by the spray. In fact, several collections 2 weeks after the spraying were larger in area D than in E. The box area samples averaged about 18 individuals per collection for *D. inversa* and 4 for the other species. Not affected.

HYMENOPTERA

Xiphydriidae

Xiphydria champlaini Roh. Two specimens were taken in area D on June 22.

Tenthredinidae

Scattered adults of 8 genera were taken in both areas before the spraying but not afterwards. Adults of *Macrophya trisyllaba* Nort. were rather common in area D a few days before the spraying, but only 2 were taken in an hour of collecting 2 weeks later. Small numbers of tenthredinid larvae were present in both areas after the spraying.

Braconidae

Alysiinae and Aphidiinae. In area D each group averaged 20 specimens per hour of sweeping 2 days after the spraying, after which only a few were collected until July 22, at which time the collections were large again.

Aphaereta muscae Ashm. This species was probably greatly reduced, for only 3 specimens were taken in 10 box area samples in area D, 2 weeks after the spraying, compared with 48 from a similar number of samples from area E.

Ascogaster sp. Very common on rank vegetation in area D before the spraying, but was not noticed again 2 weeks later.

Macrocentrus sp. Emergence began about 2 weeks after the spraying, and several times more specimens were collected in area D than in E.

Meteorus sp. Sweep collections suggest that the spray caused a great reduction in numbers.

Microbracon sp. Several swept from area D about 3 weeks after the spraying.

Microgasterinae. Present in both areas around spraying time and were particularly abundant in area D, 3 or more weeks later.

Opius sp. This genus was as abundant or more so in area D than in area E 3 weeks or more after treatment.

Sigalphinae. Not abundant in either area until June 22 and after, when some sweep collections averaged 60 specimens per hour.

Spathius sp. This species did not occur in significant numbers until early July, when it was moderately common in both areas.

Certain of the braconids emerging near spraying time were reduced in numbers, whereas those appearing 2 weeks or more later were not affected.

Ichneumonidae

Over 70 genera were represented in sweep collections, of which about 25 were not taken until a week or more after the spray application. Usually the species in each collection were represented by only 1 or 2 specimens. Most of those swept in area D before the spraying were not collected again afterwards. *Coccygomimus aequalis* (Prov.) was taken at the rate of 8 specimens per hour in area D about 3 weeks after the spraying, compared with 1 per hour in area E. A species of *Gelis* was equally abundant in both areas late in June. Scattered specimens of *Megarhyssa* sp., *Phobocampe* sp., *Stilpnus* sp., *Xestophyes* sp., *Horogenes* n. sp., and *Neogreeneia picticornis* Vier. were

present in area D, 3 weeks after the spraying. It appears that many of the ichneumonids were temporarily reduced in numbers as a result of the DDT spray.

Diapriidae

Although these forms averaged about 20 specimens per hour in sweeps from both areas before the spraying, there was a marked reduction in numbers afterwards, especially in area D. Two weeks after treatment, however, collections averaged 32 per hour in area D and only 2 per hour in area E. *Xenotoma* sp. was the most abundant species in the box area traps, its numbers 2 weeks after the spraying being about 7 times greater in area D than in E.

Serphidae

Phaenoserphus abruptus (Say). Box-area-trap samples taken 2 weeks after the spraying indicated that this species was twice as abundant in area E as in D.

Platygasteridae

Although members of this family were abundant in both areas before treatment, only a few were taken afterwards, the majority being in area E.

Cynipidae

This family did not appear to be adversely affected by the spraying, as indicated by small numbers taken in sweeping.

Chalcidoidea

These parasites averaged 20 specimens per hour in sweeps in both areas before the spraying. During the last half of June, 5 to 12 per hour were swept in area D and none in area E.

Formicidae

Aphaenogaster spp. According to ground-trap collections, members of this genus, including *A. treatae* Forel, were not adversely affected by the spray (table 16).

Camponotus caryae subbarbatus Emery. Sweep collections ranged from a few to 40 per hour in both areas, and it is doubtful that this species was reduced much by the spray, unless perhaps immediately after the application.

Formica exsectoides Forel. Ground-trap collections showed no reduction after the spraying (table 16). In 6 colonies in area D, where the ants were evenly distributed over the domes of the nests, counts made before the spraying ranged from 18 to 50 individuals per square foot. About 2 weeks after treatment, there was practically no reduction in numbers in 4 nests, but in the other 2 only a comparatively few ants were present. It is doubtful, however, that the spray caused any significant change in population.

Formica fusca var. *subsericea* Say. Counts of ants were made as they crawled near nest openings on a sunny day, 5 days before and then again about 2 weeks after the spraying. All counts were lower after the spraying, but when one of the nests was opened it contained a large number of ants. It seems probable that this species was not affected much by the spray.

Lasius niger (L.) vars. Both ground-trap (table 16) and sweeping records indicate no reduction in population attributable to the spray. Sweep collections sometimes averaged over 100 ants per hour.

Leptothorax curvispinosus Mayr. It is doubtful that this species was reduced in numbers by the spray, although only a few specimens were taken in area D, 1 week afterwards.

Myrmica spp. This species was first collected in areas D and E 1 week after the spray application. Later collections were approximately of equal numbers.

Prenolepis imparis (Say). Ground-trap collections (table 16) suggest this species was greatly reduced by the spray, but sweeping records, which ranged from a few to over 200 specimens per hour, do not support this idea. It was clearly evident that a high population of this species was still present in area D after the spraying.

Tapinoma sessile (Say). This species was probably moderately reduced in numbers for a week after the spraying (table 16).

In general it appears that several species of ants may have been initially reduced in numbers by the spray, but the residual DDT did not affect them a week later.

Vespidae

Polistes fuscatus (F.). Several seen in area D about 2 weeks after the spraying.

Vespula maculifrons Roh. Two specimens taken in the sprayed area on July 2.

Halictidae

Halictus sp. A number of specimens were swept from both areas 1 week after the spray application, and later.

Bombidae

Bombus spp. Six specimens were observed in flight in area D within 2 weeks after the spraying.

ARACHNIDA

ARANEIDA

Theridiidae

Theridion frondeum Hz. This species was not affected by the spray, and about 3 weeks afterwards sweep collections averaged about 15 specimens per hour in both areas.

Thiodina sylvanica (Hz.). Occurred in about equal but small numbers in sweeps made in both areas before the spraying and a week later.

A few specimens of 2 other species, *Theridula opulenta* Walck. and *Dipoena nigra* (Em.), were taken about 2 weeks after the spraying in area D only.

Argiopidae

Leucauge venusta (Walck.). This species was collected at the rate of 8 specimens per hour of sweeping and did not appear to be reduced in numbers by the spraying.

Pisauridae

Dolomedes sp. Meager sweep collections suggested that there was a reduction in numbers for several weeks after the spraying in area D.

Pisaurina mira (Walck.). Seven sweep collections made in June averaged 11 specimens per hour, and there was no significant difference between the numbers taken in areas D and E at any time after the spray application.

Lycosidae

Specimens of *Pirata* sp. and *Pardosa* sp. were taken infrequently in both areas.

Mimetidae

Mimetus interfector Hz. Taken infrequently by sweeping, mostly in area D after the spray application.

Thomisidae

Misumenops spp. Two species were taken infrequently by sweeping in both areas.

Philodromus ornatus Hz. A few specimens were taken after the spraying, mostly in area D.

Clubionidae

Anyphaena sp. Seven specimens were taken in area D, 5 days before the spraying but none afterwards.

Anyphaena pectorosa Koch. Sweep collections in area D averaged about 7 specimens per hour, 1 to 3 weeks after the spraying, but the species was not taken in area E until June 25.

Salticidae

Dendryphantes capitatus (Hz.). Equally prevalent in sweeps in both areas a few days after the spraying.

Zygoballus betteni Peck. Common in sweeps in both areas after the spraying, especially in area D.

Wala mitrata Hz. A few specimens were taken in sweeps after the spraying in area D only.

Phalangiidae

Leiobunum spp. Both ground-trap (table 16) and sweeping collections showed these forms to be greatly reduced by the spray. Areas D and E averaged about 70 specimens per hour of sweeping before the spraying, and whereas collections at intervals after the spraying in area E ran as high as 194, only 1 or 2 were taken in the sprayed area at the same time. Thus these arachnids were almost eliminated by the spray.

The spray of 2 pounds of DDT per acre did not cause much change in the spider population. Except for species of *Leiobunum*, which were almost eliminated by the treatment, other species were not affected.

SUMMARY AND CONCLUSIONS

In late May and early June 1945, 3 sizable forest areas were treated with experimental dosages of DDT by airplane to determine the effects of the toxicant on arthropods and other animals. Area A of 1,200 acres is in a mountainous section covered with sapling growth, and area C of 350 acres is in a rather open mature forest with considerable undergrowth, both of which are located near Scranton, Pa., whereas area D of 117 acres is in a mature deciduous bottomland forest located near Bowie, Md. Suitable control areas were selected for comparison with study areas A and D. Areas A, C, and D were sprayed by airplane with DDT-oil solution at the rates of 5, 1, and 2 pounds of DDT per acre, respectively.

Numerous objective sampling methods were used for about 4 months in area A, 1 month in area C, and 6 weeks in area D to follow the effects of the treatment on the faunas present. Area A was given some study again the following season. General observations augmented the routine sampling procedure. Several hundred species were observed individually, whereas much of the remaining fauna was studied as larger units, such as genera, families, and orders. Data for the more abundant species have been condensed in the appended tables. Other information on various species and groups is summarized in annotated lists of the invertebrates studied, which have been arranged in systematic order.

Arthropods showed great variation in susceptibility to DDT as it was applied in these experiments. In most cases this variation may be due to the differences of opportunity to contact DDT, as governed by individual ecology, habits, seasonal life history, and structure. In general the species exposed on vegetation were more affected than those protected under bark scales, in burrows, in leaf mold and soil, and in similar places. The timing of the spray application was important. A large portion of those that were caught in a susceptible stage (such as caterpillars and flying adults of Diptera and parasitic Hymenoptera) when the spray was applied were severely affected. Species partially and entirely in a protected stage at the time of application and during the period when the residual toxicity was effective were relatively immune. The extremely hairy species (Lepidoptera and bees) seemed resistant to the treatment.

All dosages caused an almost immediate and pronounced effect on many species of insects. The residual toxicity of DDT in the 1-pound-per-acre treatment lasted for about a week, while the residual effect of the 5-pound-per-acre dosage was severe after 6 weeks, with little recovery in the fauna until after 3 months. This heavy dosage was applied before the leaves were well out, which permitted a thorough coverage of the forest and accentuated the effects of a heavy dosage. With the 2-pound dosage the exposed fauna took 2 weeks to approach normal numbers again, but for some species the effects of the treatment were noticeably longer.

In area A small caterpillars on the foliage of the trees were eliminated soon after the spray application, while those on undergrowth were at first much reduced but by the end of summer had regained normal numbers. Adult moths, particularly the larger species, seemed relatively immune to the residual DDT. Membracids, some cicadellids, and leaf-eating beetles were greatly reduced, while some tree-inhabiting species, including psyllids, Collembola, scale insects, and aphids, were unaffected or increased in numbers. Diptera and Hymenoptera (except bees) were especially susceptible to the treatment, but many nemocerous Diptera living in leaf mold and in other secluded places continued successful breeding. Most Hymenoptera parasitic on Lepidoptera were almost exterminated, but many parasitic on Nemocera and Syrphidae continued to be common. Some of the ground arthropods—daddy longlegs, larger diplopods, and carabids—were nearly exterminated while others survived. Humus and soil arthropods seemed unaffected. Among the spiders, the orb-weaving and other exposed species were almost eliminated. Species on the ground and under stones and bark were mostly unaffected.

About a month after the spray application a severe outbreak of aphids developed, including many species infesting a variety of trees. This increase was due apparently to the greater effect of DDT on the aphid parasites and predators than on the aphids. Following closely the outbreak of aphids, their parasites and

predators greatly increased in numbers, but were unable to reduce the outbreak until after a heavy rain had killed a large percent of the aphids.

Another notable effect of the treatment in area A was a tremendous increase of mites on foliage, presumably as a result of reduction of their predators. One species became exceedingly abundant 2 months after the spraying, but did not reach its largest numbers until the following May, when the infestation caused serious blotching of red maple leaves.

The effects of the treatments of 1 and 2 pounds of DDT per acre were not prolonged and most of the arthropods studied seemed to be present in usual numbers 2 or 3 weeks later. Both dosages killed most of the caterpillars and in the 2-pound-per-acre area aphids probably increased following the spraying. Adult insect parasites and predators emerging a week or more after these sprayings did not appear much affected by the residual spray. Calypterate flies proved very susceptible to the 2-pound dosage, showing an over-all reduction of about 85% for 2 months afterwards.

These studies should be considered as being preliminary. Unknown biological relationships, including life histories, habits, predation, and parasitization, made it difficult to estimate properly the effects of aerial applications of DDT on many forest invertebrates. Future studies are needed to evaluate the effects of several dosages on faunas in different forest types having variable canopy densities. Additional studies on the effects of DDT sprays on the interrelationships of insects and their natural enemies—insects, amphibians, reptiles, fish, birds, and mammals—would be of great interest and value. An ideal arrangement would be to treat at least several square miles of forest with DDT dispersed within a few days from large airplanes, and to study the fauna near the center so as to minimize the immigration factor. Heretofore uneven spray distribution and immigration of insects from nearby untreated forests have tended to obscure some of the relationships studied on relatively small areas.

General conclusions indicated by the work to date are that a single airplane application of DDT to a forest at the rate of 1 pound per acre—enough to control many forests pests—does not seriously damage the general arthropod fauna, although a few species would probably be exterminated by a thorough application at this rate. An application of 5 pounds of DDT per acre threatens near extermination of many harmless or beneficial species, and may result in harm to the forest through encouragement of aphid and mite outbreaks. DDT used at moderately light dosages will tend to restrict the range and abundance of many harmless and beneficial species, and its widespread use on forest threatens extermination to some of the more susceptible and sedentary species. However, even with a dosage of 5 pounds of DDT per acre, the effect on the arthropod fauna as a whole is far from being calamitous.

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THE LOCAL DISTRIBUTION AND ECOLOGY OF THE PLETHODONTID SALAMANDERS OF THE SOUTHERN APPALACHIANS

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A dissertation accepted by Northwestern University in partial fulfillment of the requirements for the degree Doctor of Philosophy.

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THE LOCAL DISTRIBUTION AND ECOLOGY OF THE PLETHODONTID SALAMANDERS OF THE SOUTHERN APPALACHIANS

INTRODUCTION

The salamanders of the family Plethodontidae provide good opportunities for studies of comparative ecology. They are well known taxonomically, and the geographic ranges of most of the species have been worked out in considerable detail. This permits accurate field identification of nearly all species, an advantage of major importance in studying local distribution and field activity. With a few exceptions, these salamanders have not been studied carefully from the ecological standpoint.

The place of origin of the Plethodontidae is generally considered to be the Appalachian highlands, which is also the region of maximum diversity of forms. This area is clearly the optimum one for an ecological investigation of the group. Within the family, the genus Desmognathus offers the best material for such a study for several reasons:

1. Within the genus, there is a complete range from aquatic to terrestrial species, offering an exceptional opportunity for a study in comparative ecology.
2. As many as four species are to be found in the same locality.
3. Most of the species are abundant throughout the region under consideration—a significant advantage in any sort of quantitative study. For these reasons, this work has centered around the species of Desmognathus, but other genera were also investigated, and points clearly illustrated by them have been included.

I am indebted to a number of people for assistance during this investigation. Part of the work was carried out with the help of a University of North Carolina scholarship to the Highlands Biological Laboratory. For this, I am grateful to Professor J. N. Couch, Director of the laboratory, and to Miss Thelma Howell, Resident Director. Dr. W. L. Engles of the Department of Zoology, University of North Carolina, helped with the identification of some of the specimens.

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The following were most helpful in granting collecting permits: Mr. C. N. Mease and Mr. B. Rector, wardens for the Mount Mitchell Game Management Area; Mr. F. Wilson, warden for the Mount Mitchell State Park; Mr. T. Wilson, U. S. Forest Service Warden for Cane River Valley; Mr. Weldon Weir, Manager, Public Works Department, City of Asheville, N. C., and Mr. Thad Burnett, Superintendent of Watersheds, City of Asheville. Mr. Burnett, Mr. Rector, and Mr. T. Wilson were especially kind in giving invaluable information concerning trails and other local geography.

Finally, I am indebted to Professor Orlando Park of the Department of Zoology, Northwestern University, for advice, encouragement, and criticism in directing this research.

REVIEW OF THE LITERATURE

The Salamanders

Taxonomic order must precede ecological studies if the latter are to have validity. The stable condition of the systematics of the Plethodontidae is largely due to the work of E. R. Dunn, culminating in his monograph of 1926. Since then, only three species and four subspecies have been added to the twenty-two Southern Appalachian forms recognized by Dunn.

The detailed life-history studies of the type represented by Wilder's work on *Desmognathus fuscus* have never been extended to the salamanders of the present region. The egg-laying habits of several species were described by Pope (1924), but most ecological observations have been made sketchily, since the authors were more interested in taxonomy and phylogeny.

As might be expected in a mountainous region, all collectors in the Southern Appalachians have been assiduous in their attempts to correlate the distribution of salamanders with altitude. The results have nearly always been disappointing, especially so the work that has attempted syntheses of data from different localities. The difficulty comes from two main sources. First, the mountains are only high enough to support two major kinds of forests, and second, the random assembling of data from various localities has not taken into account the differences between the localities or between the subspecies of salamanders. This has led to repeated statements that many species have widely overlapping vertical ranges, when in fact they may not, as careful analysis shows.

The most thorough analysis of vertical distribution in the Southern Appalachians is that of King (1939) for the Great Smoky Mountains. While his charts do not take into account the differences between localities, the text mentions them in some instances.

The only study of salamander distribution includ-

ing a careful vertical transect on one face of a mountain has been by Schmidt (1936) for the tropical genus Bolitoglossa (=Oedipus). His demonstration of correlations between vertical distributions of salamanders and vegetation zones shows what can be done by means of the transect technique. Schmidt also was able to demonstrate that the vertical distribution of at least one species *(B. franklini)* was different on two separate mountains. He thus showed the danger of synthesizing data from varying localities.

Although all of the authors concerned with Southern Appalachian salamanders were aware that ecological differences existed between the species, they were of varying opinions as to the exact nature of these differences. Noble (1927) and Dunn (1926, 1928) were at variance as to the types of streams selected by two species of Desmognathus. Bishop (1928) was cautious as to these ecological differences, indicating that they were apparent to him only in the larger streams.

Two types of ecological differences between species of Desmognathus have been reported. These are degree of proximity to water, and type of stream selected. None of the authors made systematic records of the precise locations of individuals, and the reports are the results of general impressions gained in the process of collecting.

With regard to activity studies, none have been carried out systematically to determine the pattern. Although many investigators have made use of the nocturnal habits of Plethodontidae to collect specimens, there are no records of comparisons between species with regard to the degree of nocturnality exhibited. The work of Park (1931-1947) has demonstrated the value of recording physical influences of the environment in connection with activity studies. In a recent paper, he describes a method of determining quantitatively the degree of nocturnality or diurnality exhibited by an animal (Park 1941).

The influence of the physical environment on the distribution and activity of salamanders, while often mentioned (Noble 1927, e.g.), has not received the detailed attention that it deserves. Shelford (1913, 1914) demonstrated differences between *Plethodon glutinosus* and *P. cinereus* in reaction and susceptibility to dry air, and correlated these differences with the distribution of the two species. More recently, Burger (1935) and Littleford, Keller, & Phillips (1947) have shown differences in resistance to water loss between *Plethodon cinereus* on one hand and *Desmognathus fuscus* and *Eurycea bislineata* on the other. This difference is also correlated with ecological distribution.

The place of salamanders in the food cycles of their communities has been studied by a number of investigators. The information indicates that salamanders will devour almost any organism that falls within a reasonable size range, and are thus not restricted to a habitat because of a specific food. As regards the enemies of salamanders, less information is available, but in general salamanders are fed upon by almost any carnivorous species that is able to catch them.

They occupy intermediate positions in the food webs of the communities in which they live, preying on herbivores and small carnivores, and becoming the prey of still larger carnivores. In the Southern Appalachians, where they are the most abundant members of the vertebrate fauna, the Plethodontidae must occupy an important place in the community economy.

THE REGION

Dunn (1926) has indicated the Appalachian highlands as the place of origin of the family Plethodontidae. This is the region where the most primitive forms are found, and where primitive species still occupy the original habitat niche—the mountain brooks. As Dunn points out, this is more or less contrary to the theory of W. D. Matthew (1915) that primitive forms are to be expected at the periphery of the range. Matthew's theory, however, is tenable only if the climate has changed at the place of origin, and mountains have been in existence in the region in question since the close of the Paleozoic Era, or throughout much more time than is encompassed by the probable evolution of the Plethodontidae. Consequently, the region has been high and humid continuously, and the mountain brook habitat has always been available, permitting the retention of the primitive forms, such as Gyrinophilus, at the place of origin of the family. All authorities are agreed that the Plethodontidae arose as forms specialized for an existence in mountain streams. Only those that have acquired the ability to live on land have been able to move any appreciable distance from this center; it is significant that all aquatic and semi-aquatic species are still confined to eastern North America. Cain (1943) has recently shown that the cove hardwood forests of the Southern Appalachians are nearly identical with the widespread forests of Tertiary times. This might explain the retention of certain primitive terrestrial forms, such as *Plethodon yonahlossee*, in this region.

The plant habitats of this region have received more attention than have the animals present in them. The most complete classification of the forest types is to be found in Frothingham *et al.* (1926). Cain's analyses of the flora of the Great Smoky Mountains are important contributions to the plant ecology of the region. Davis (1930) made a detailed study of the vegetation of the Black Mountains of North Carolina.

DESCRIPTION OF THE LOCALITIES STUDIED

THE BLACK MOUNTAINS AREA

All of the places studied are located in the Southern Appalachians. They are in western North Carolina, northwestern South Carolina, and northern Georgia (Fig. 1). The majority of the observations were made in the Black Mountains, which are located in Yancey County, North Carolina, overlapping slightly into Buncombe County. They lie within the

quadrangle enclosed by 35° 42′ and 35° 55′ north latitude and 82° 12′ and 82° 30′ west longitude. This range of mountains is the highest in eastern North America, reaching an elevation of 6,684 feet above sea level at the top of Mount Mitchell. No point along the entire length of the range lies below 5,300 feet, and fourteen peaks rise above 6,200 feet.

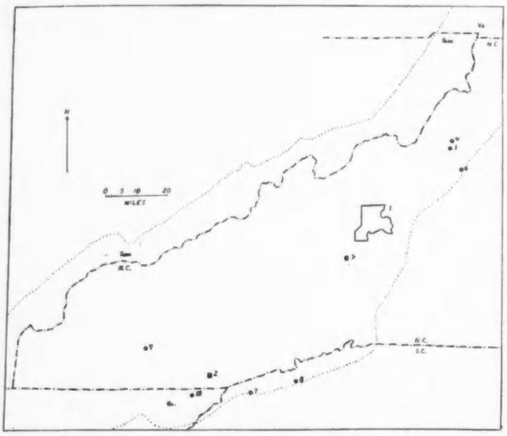

FIG. 1. Map of western North Carolina and adjacent parts of other states, showing localities studied thoroughly (open), fairly well (squares), and briefly (circles). 1. Black Mountains Area; 2. Highlands; 3. Patton Cove; 4. Grandfather Mountain; 5. Grandmother Mountain; 6. Mortimer; 7. Jocassee; 8. Table Rock State Park; 9. Wayah Bald; 10. Rabun Bald. Dotted line indicates approximate boundary of Southern Blue Ridge Physiographic Province.

The area herein referred to as the Black Mountains Area includes the southern half of the Black Mountains, plus the adjacent section of the Blue Ridge Mountains, including the associated valleys. The Blue Ridge Mountains, which form the divide between Gulf and Atlantic drainage systems, lie immediately to the east of the Black Mountains.

The lowest elevation in the Black Mountains Area is 1,900 feet above sea level at the eastern foot of the Blue Ridge. The principal streams in the area are the North Fork of the Swannanoa River, which drains the south side of the Black Mountains, Cane River, which drains the west side of the Blacks, the South Toe River, which drains the north and east sides of the Blacks and the west side of the Blue Ridge, and Buck Creek and Curtis' Creek, both of which drain the east side of the Blue Ridge.

While no detailed study was made of the plant habitats of the Black Mountains Area, it is important to locate the approximate local distribution of the major kinds of forests, since some species of salamanders are confined to single habitats, or at least show a marked preference for them. These habitats conform to the ones described for the Southern Appalachians in general. There are five of them, the three major ones being northern hardwoods, cove hardwoods, and spruce-fir. The beech gap and heath bald habitats are much more restricted in area.

The subalpine spruce-fir forest, consisting mainly of red spruce (*Picea rubens* Sargent) and Fraser's fir (*Abies Fraseri* (Pursh) Poir.), is found on top of the Black Mountains and in one restricted area in the Blue Ridge. It extends down the side of the Blacks variably. In Middle Creek watershed, this forest descends to an elevation of 4,500 feet; in the valley of the North Fork of the Swannanoa River, it descends to 5,300 feet, and elsewhere it is restricted to elevations above 6,000 feet on the eastern slope of the range, while on the western slope the spruce-fir forest is absent, save for the very tops of the mountains. This distribution is clearly correlated with past timbering. Of the whole area, only a few relatively small areas remain virgin forest, the rest having been cut, mostly during the first fifteen years of the present century. The areas reported to be virgin are Middle Creek watershed, part of the watershed of the North Fork of the Swannanoa River, and a small area including the top of Mount Mitchell. Timbering has brought about at least one major change in the plant habitats of the region. This is the introduction of a zone of fire cherry (*Prunus pennsylvanica* L. f.) or mixed fire cherry and yellow birch (*Betula lutea* Michx. f.) in areas where fire has followed the cutting of the spruce-fir forest. This is now a characteristic zone of vegetation in the Black Mountains. It lies above the cove hardwoods and below the spruce-fir at elevations between 4,500 and 6,000 feet in the east side of the range, and runs up nearly to the top of the ridge on the west side. No such zone is to be found in the untimbered localities at the same elevations.

The northern hardwoods occupy the ridges at elevations between 3,500 and 5,000 feet. This forest was formerly dominated by the chestnut (*Castanea dentata* (Marsh.) Borkh.), but at present oaks (*Quercus* spp.) and hard maples (*Acer* spp.) are the dominant trees.

The cove hardwoods occupy the greater part of the area. This habitat is dominated by hemlock (*Tsuga canadensis* (L.) Carr), beech (*Fagus grandifolia* Ehrh.), maple (*Acer* spp.), and tulip poplar (*Liriodendron tulipifera* L.) in varying proportions and combinations. Within the study area, the forest under discussion has a vertical range from 1,900 feet in Buck Creek valley to 5,300 feet in the valley of the North Fork of the Swannanoa River. It seems to be restricted to the more moist areas, hence its name.

The heath bald, dominated by members of the family Ericaceae, is restricted to a few subsidiary ridges extending eastward from the main ridge of the Black Mountains proper, and on these ridges is confined to elevations between 5,000 and 5,500 feet.

The beech gap forest in this area is confined to localities not studied for the salamander fauna.

OTHER AREAS

In addition to the main study area, observations were made at a number of other localities in the Southern Appalachians.

Highlands is located in southeastern Macon County, North Carolina. It lies on the Blue Ridge at an elevation of 4,000 feet. Two small localities were studied. The first of these, Horse Cove, lies immediately east of the town, and belongs to the Atlantic drainage system, its small creek being a tributary of the Chatooga River. The second Highlands locality, a small branch on the south side of Bearpen Mountain, lies within the Gulf drainage system at an elevation of 4,000 feet. At both locations, the forest is of the cove hardwoods type.

Patton Cove is on the north side of the Swannanoa Mountains in eastern Buncombe County, North Carolina near the town of Swannanoa. It belongs to the Gulf drainage, and ranges in altitude from 2,300 to 4,000 feet. The cove hardwoods are mixed with open pasture and orchards.

The remaining localities, listed below, were visited briefly. Following each is given its approximate elevation and forest type. Grandfather Mountain, Avery County, North Carolina, 4,500-5,900 feet, spruce-fir and heath bald; Grandmother Mountain, Avery County, North Carolina, 4,100-4,686 feet, cove hardwoods and heath bald; Mortimer, Caldwell County, North Carolina, 1,500 feet, cove hardwoods; Jocassee, Oconee County, South Carolina, 900 feet, transition between cove hardwoods and Piedmont oak-pine; Table Rock State Park, Pickens County, South Carolina, 1,200 feet, cove hardwoods; Wayah Bald Mountain, Macon County, North Carolina, 3,500-4,100 feet, cove hardwoods and northern hardwoods; and Rabun Bald Mountain, Rabun County, Georgia, 3,600 feet, cove hardwoods. The Rabun Bald and Wayah Bald localities are in the Gulf drainage. All of the rest are in the Atlantic drainage.

SYSTEMS OF COLLECTING

Nearly all previous work involving the vertical distribution of salamanders has been based on assembling isolated observations from localities scattered over a large area. The notable exception is Schmidt's work, based primarily on a vertical transect of a single Guatemalan volcano (Schmidt 1936). This type of investigation is highly desirable, since the bringing together of scattered records can lead to erroneous conclusions. Bailey (1937) found that *Plethodon metcalfi* was separated into large and small forms on the basis of altitude. This observation was based on high altitude specimens from one locality (Black Rock) and low altitude specimens from another (Swannanoa). These two areas are now known to lie in the ranges of different species (Grobman 1944. Hairston & Pope 1948). The vertical distribution of salamanders may vary considerably on different sides of the same mountain, as will be demonstrated later.

The transect method was used to determine the local distribution of salamanders in this study. Collections were made along these transects at vertical intervals of 50 to 250 feet. The original plan called for collections at hundred-foot intervals, but this was not feasible in the area studied, because of high waterfalls in some places and rhododendron thickets in others.

VERTICAL TRANSECTS

Eight vertical transects were employed in studying the local distribution of the Plethodontidae. Four of these were made in the summer of 1940, three being repeated several times in the summer and fall of that year. These three form a continuous series from the highest to the lowest elevation in the Black Mountains Area.

The first transect began at the headquarters of the Mount Mitchell Game Management Area, near the confluence of Neal's Creek and the South Toe River at an elevation of 3,000 feet. From this point, the trail up Mount Mitchell was followed. This trail ascends the ridge known as Little Mountain to an elevation of 5,700 feet, where it joins the old grade of a logging railroad to the site of Camp Alice, on Lower Creek at an altitude of 5,790 feet; from there it proceeds directly to the tower at the top of Mount Mitchell. The second transect also started at the game management headquarters; it followed Neal's Creek to its source, a spring at Big Laurel Gap in the Blue Ridge at an elevation of 4,100 feet. The third transect began at Big Laurel Gap and descended the east face of the Blue Ridge via United States Forest Service roads to Sugarcove Gap and thence to an elevation of 1,900 feet in Duncan Cove, a part of the valley of Buck Creek. In 1940, two transects were made of Patton Cove, described previously.

The only transect made in 1946 was of Horse Cove, Highlands, N. C., covering an altitudinal range from 3,000 to 4,000 feet.

The results of observations made in 1940 and 1946 indicated the necessity of taking into account the exposure of the slope or cove being studied. With this in mind, three more vertical transects were made in the summer of 1947. The exposures chosen were south-facing, north-facing, and east-facing. The south-facing cove was the valley of the North Fork of the Swannanoa River. This transect began at an elevation of 2,400 feet and followed the stream via the East Prong and Big Branch to the top of Potato Knob, 6,400 feet above sea level. Cane River Valley was selected as the north-facing cove. The transect started at 3,000 feet and followed the stream up Blue Sea Fork and a branch of this creek to the top of Blackstock Knob, at an elevation of 6,350 feet. The east-facing cove of Middle Creek was the last vertical transect made. Starting at the confluence of this stream and the South Toe River, it followed the creek and its north branch to the top of the Black Mountains between Potato Hill (not Potato Knob, mentioned previously) and Cattail Peak. The vertical range of this transect was from 2,750 to 6,200 feet.

All of the vertical transects were made using a Taylor Aneroid Altimeter, Model No. 2075 FK. This instrument was set at a United States Geological Survey bench mark at the beginning of each day, and checked against a known elevation at the end of the

day. No discrepancies of more than 25 feet were noted on any of these check readings.

HORIZONTAL TRANSECTS

In four of the coves chosen for vertical transects, horizontal transects were made along with the vertical ones. The coves were the ones studied in the summers of 1946 and 1947. At each elevation, collections were made beginning in the stream and extending away from it for a distance of 200 feet. As each salamander was collected, its species and position relative to the stream were noted. Between the banks of the stream, two types of position were recognized: salamanders that were actually in the water when collected, and those on non-inundated parts of the stream bed. The latter were on sand or gravel banks or under debris on top of boulders. For salamanders not within the banks of the stream, the distance from the nearest visible water was recorded. Distances up to ten or fifteen feet were measured with a marked stick. Longer distances from the stream were paced off.

OBSERVATIONS

SPECIES OBSERVED

Twelve species and subspecies of Plethodontidae were collected in the Black Mountains Area. They were:

Gyrinophilus danielsi danielsi (Blatchley)
Gyrinophilus danielsi dunni Mittleman and Jopson
Pseudotriton ruber nitidus Dunn
Eurycea bislineata wilderae Dunn
Desmognathus quadra-maculatus (Holbrook)
Desmognathus monticola Dunn[1]
Desmognathus ochrophaeus carolinensis Dunn
Desmognathus wrighti King
Leurognathus marmorata Moore
Plethodon yonahlossee Dunn
Plethodon glutinosus (Green)
Plethodon metcalfi Brimley.

Four additional species have ranges that indicate that they might be found in the Black Mountains Area. They are *Desmognathus fuscus fuscus* (Rafinesque), *Plethodon cinereus cinereus* (Green), *Pseudotriton montanus montanus* (Baird), and *Eurycea longicauda guttolineata* (Holbrook). None of them, however, has been reported from this locality, and a close examination of their stations indicates that they probably do not occur here. The only truly montane records of *D.f. fuscus* are from the Great Smoky Mountains, where King (1939) reports the species from as high as 5,000 feet. This is from the Tennessee side of these mountains, an area sufficiently distant from the present area to account for differences. The other montane records are from broad valleys on plateaus, a type of physiography not found in the Black Mountains Area. *Plethodon cinereus* is the most likely candidate for inclusion, since it is not uncommon at Grandfather Mountain to the northeast, but this is approaching the southern limit of its range, and it may really be absent. *Pseudotriton montanus* and *Eurycea l. guttolineata* are really Piedmont salamanders, and the few montane records for them are like most of the ones for *Desmognathus fuscus*. None of the four possible omissions can be anything more than very rare in the Black Mountains Area, or the present study would surely have shown their presence, as it has the even rarer *Leurognathus marmorata* and *Plethodon yonahlossee*.

The remaining areas were studied for shorter periods of time, and the lists are of positive value only. The salamanders found at each locality were as follows:

Patton Cove
Desmognathus quadra-maculatus (Holbrook)
Desmognathus monticola Dunn
Desmognathus ochrophaeus carolinensis Dunn
Pseudotriton ruber nitidus Dunn
Plethodon glutinosus (Green)

Highlands
Desmognathus quadra-maculatus (Holbrook)
Desmognathus monticola Dunn
Desmognathus ochrophaeus carolinensis Dunn
Pseudotriton ruber schencki (Brimley)
Plethodon shermani melaventris Pope & Hairston

Grandfather Mountain
Desmognathus ochrophaeus carolinensis Dunn
Desmognathus wrighti King
Plethodon metcalfi Brimley
Plethodon welleri Walker

Grandmother Mountain
Desmognathus ochrophaeus carolinensis Dunn
Plethodon glutinosus (Green)
Plethodon metcalfi Brimley

Mortimer
Desmognathus quadra-maculatus (Holbrook)
Plethodon yonahlossee Dunn

Jocassee
Desmognathus quadra-maculatus (Holbrook)[2]
Desmognathus ochrophaeus carolinensis Dunn
Eurycea bislineata wilderae Dunn
Plethodon glutinosus (Green)
Plethodon shermani clemsonae Brimley
Plethodon shermani melaventris Pope & Hairston[2]

Table Rock State Park
Desmognathus ochrophaeus carolinensis Dunn
Plethodon shermani melaventris Pope & Hairston

Wayah Bald
Desmognathus quadra-maculatus (Holbrook)
Desmognathus ochrophaeus carolinensis Dunn
Plethodon shermani shermani Stejneger

Rabun Bald
Desmognathus quadra-maculatus (Holbrook)
Desmognathus monticola Dunn
Desmognathus ochrophaeus carolinensis Dunn
Plethodon shermani rabunensis Pope & Hairston

VERTICAL DISTRIBUTION

There are no differences in the vertical distribution of the six genera observed. Only Leurognathus is confined to the altitudinal range studied, and it is not separated vertically from any other genus. When the species are plotted against altitude (Fig. 2), differences in vertical range appear within the genera.

[1] Known for many years as *D. phoca* (Matthes). Grobman (1945) has shown that *phoca* is almost certainly a synonym of *D. fuscus*.

[2] Actually from an elevation 700 feet above Jocassee, at the top of the Lower Falls of the Whitewater River.

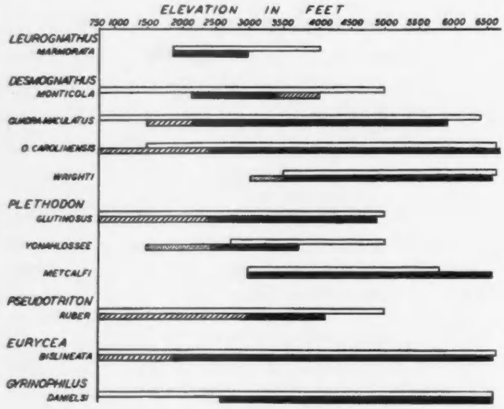

FIG. 2. Vertical distribution of the species of Plethodontidae. Solid bars represent observations in the Black Mountains Area; stippled bars represent exceptional extensions (see text); cross-hatched bars represent extensions from other areas studied; open bars represent vertical distribution as recorded in the literature.

Making allowances for differences in locality, there is good agreement between my observations and those of previous authors, with the exception of *Plethodon yonahlossee*. This discrepancy will be considered later.

In Desmognathus, there is a trend vertically along the series *D. monticola-quadra-maculatus-carolinensis-wrighti*, but the overlap is more conspicuous than the trend, only *D. monticola* and *wrighti* being completely separated by altitude in this area.

Plethodon shows a difference between *P. glutinosus* and *metcalfi*, and between *P. yonahlossee* and *metcalfi*, but *P. yonahlossee* is completely overlapped by *P. glutinosus*. The other four genera are represented in this area by one species each.

Of the Plethodontidae present in the Black Mountains Area, only *Gyrinophilus danielsi* is represented by two subspecies. In contrast to the intergeneric and interspecific relations, these two subspecies are almost completely separated according to altitude (Fig. 3).

So far, little has been added to the knowledge of the vertical distribution of these salamanders, but an examination of the data from another viewpoint brings out some interesting facts. Most previous authors have at least mentioned the fact that *Plethodon glutinosus* and *P. metcalfi* are partly separated by altitude, but it has always been assumed that there is a wide zone of vertical overlap between their ranges. An examination of the literature indicated that more mention is made of the common presence of these two species in various localities than of their vertical separation. It should be pointed out that earlier arrangements of the taxonomy of *P. metcalfi* are incorrect, as there are three distinct forms involved among the salamanders previously called "*metcalfi*" (Hairston & Pope 1948). The typical *metcalfi* ranges to the northeast (Grobman 1944) and is the one described in this study. While *glutinosus* and *metcalfi* are unquestionably present together in some places, my observations indicate that this is a restricted phenomenon, at least in the Black Mountains Area. The combined vertical data (Fig. 2) show a vertical overlap of more than 1,700 feet, but an examination of the facts shows that this is misleading. If their vertical distribution is shown according to the various transects employed, it is found that this overlapping disappears almost entirely (Fig. 4.). In fact, there are only two places

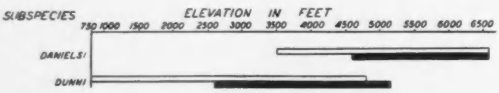

FIG. 3. Vertical distribution of two subspecies of *Gyrinophilus danielsi*. Solid bars represent distribution observed in Black Mountains Area; open bars represent distribution as reported in the literature.

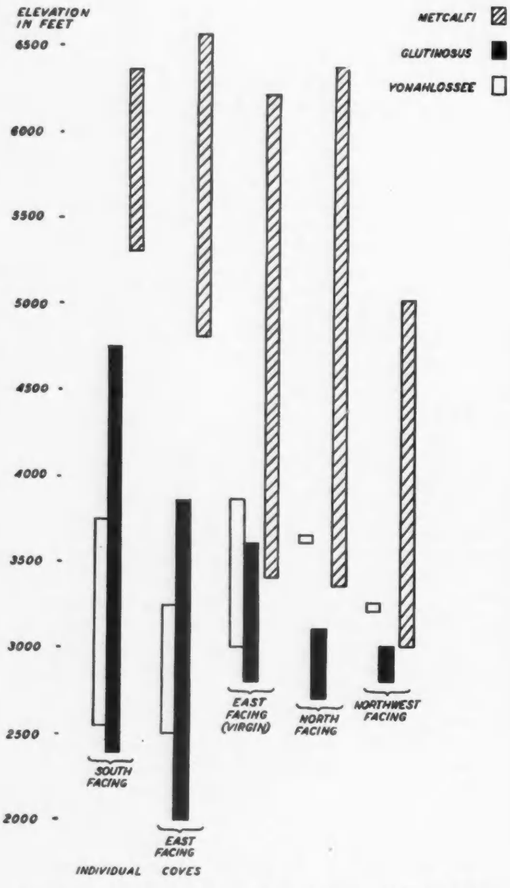

FIG. 4. Vertical distribution of three species of Plethodon in the Black Mountains Area, based on observations from individual coves. Note nearly complete separation of *P. glutinosus* and *P. metcalfi*.

in the entire Black Mountains Area where *P. glutinosus* and *P. metcalfi* are found together. These are in the virgin forest of Middle Creek watershed and in the cove of Neal's Creek near its junction with the South Toe River. The maximum vertical overlap is reduced to 200 feet in a single watershed.

The implications of these results are twofold. First, *glutinosus* and *metcalfi* must be almost exact ecological equivalents, each one being completely dominant over the other within its own range; and second, one or both species is extremely sensitive to those differences in the environment occasioned by variations in the direction in which any given cove faces. The obvious ways in which the physical environment varies in these coves are in light and temperature, but the reaction of the salamanders is probably not so simple, since temperature secondarily influences humidity, saturation deficit, and evaporation, and all of the physical influences work their effects upon the plant population.

A consideration of the problem from another viewpoint permits one to draw some valid conclusions. *P. glutinosus* is a widely distributed species, and is thus tolerant of a greater diversity of conditions than is *metcalfi*, which is restricted to the Southern Appalachians at elevations above 3,000 feet. It would be difficult to visualize a climatic or vegetational factor that prevents *glutinosus* from occupying the whole area. *P. metcalfi*, restricted as it is to an area that is primarily characterized by its high rainfall and low temperatures, is able to maintain itself better against *glutinosus* in precisely those coves where we would expect it to—the wetter, cooler, north-facing ones, and the denser and therefore more moist and cool virgin forests. It is forced to retire to higher elevations in places where these conditions do not prevail on the lower and intermediate slopes. The evidence indicates that *metcalfi* is tied to certain minimum moisture conditions that prevent its spread. On the other hand, no such mechanism is at hand to explain how this smaller form is able to prevent *glutinosus* from invading its stronghold. The explanation must lie in the complex of interrelationships that we vaguely call competition, but giving it a name does not solve the problem.

In the case of the ranges of *Plethodon yonahlossee* and *P. glutinosus*, the situation is more complicated. Their overall vertical distribution as shown in Figure 2 is completely overlapping, and the breakdown into individual coves (Fig. 4) is no more enlightening. The contrast to the *glutinosus-metcalfi* relationship is made even more surprising by the fact that *glutinosus* is more closely related to *yonahlossee* than to *metcalfi* (Dunn 1926; Grobman 1944), and would, according to Jordan's Law, be expected to be more sharply separated from it than from *metcalfi*. An examination of the data accumulated from the horizontal transects shows that the situation is not entirely without an explanation. The horizontal distributions of *Plethodon glutinosus* and *P. yonahlossee* relative to a stream are shown in Figure 5. This chart shows one striking fact. *P. yonahlossee* is not distributed at random over the forest, as might be expected of a terrestrial salamander, but is restricted to a zone within 100 feet of the stream. *P. glutinosus*, on the other hand, is distributed completely at random throughout the forest. The chart has been terminated arbitrarily at 250 feet, but *glutinosus* ranges far beyond this distance. One could wish for more *yonahlossee* records, but the species is rare, and the data are as good as could be expected. Furthermore, the nearly unanimous grouping within 60 feet gives added weight to the conclusion drawn.

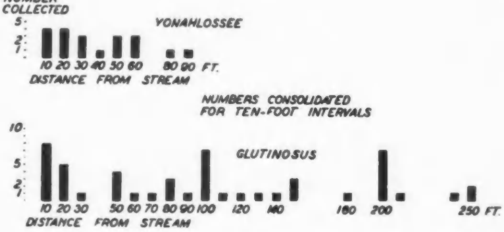

FIG. 5. Horizontal distribution of two species of Plethodon with respect to streams.

While this information does not separate the two species, it does indicate a difference between them in the zone of vertical overlap. Although the following is speculative, it would seem to be the most logical explanation of the facts. *Plethodon yonahlossee* is considered the most primitive member of the genus (Dunn 1926), and thus presumably comes closest to the ancestral Plethodon. *P. glutinosus* is the most specialized member of its species group and is thought to be of more recent origin. What one may be witnessing in the relationship of the two is the last stand of the old form in just the type of habitat to which it has been exposed longest and hence is best suited, namely, the cove hardwoods, which have changed little since Tertiary times (Cain 1943). Here, *yonahlossee* is seen as facing extinction because of the presumably better-adapted *glutinosus*, which has spread over the entire range of the former and forced it out of all but the most favorable location. In the light of this theory, it is significant that all but five of my twenty-five records of *P. yonahlossee* come from two virgin areas, the coves of Middle Creek and the North Fork of the Swannanoa River.

With regard to the overall vertical range of *yonahlossee*, some comments are in order as regards the discrepancy noted above between my records and the literature. It might be expected that the range of this salamander in the Black Mountains Area would differ from literature records in exactly the opposite way. Since this area is near the southern end of its range, *yonahlossee* theoretically should have an unusually high distribution there. I am unable to account for its apparent absence from high altitudes, but its demonstrated presence below the recorded vertical range may possibly be explained by inadequate collecting at low altitudes, a region that most collectors have neglected (Pope & Hairston 1947).

These remarks apply to all but the single lowest record. This specimen, collected at Mortimer, North Carolina, on September 12, 1940, at an elevation of 1,500 feet, comes from 1,000 feet below my next record, and 1,200 feet below any previously recorded specimen. My explanation is that this one was washed down in an exceptionally severe flood that occurred one month previously.

The subspecies of *Gyrinophilus danielsi* in the Black Mountains have a distribution pattern that is quite similar to that of *Plethodon metcalfi* and *P. glutinosus*. Gyrinophilus is difficult to obtain, and the picture is less clear, being based on only fourteen specimens from my own observations, plus Bishop's (1924) series from Mount Mitchell, and one of the paratypes of *G. danielsi dunni* from Cane River (Mittleman & Jopson 1941). The general distribution of the two subspecies (Fig. 3) shows some overlap, but data from individual coves shows them to be completely distinct (Fig. 6). *G. d. danielsi* is confined to the spruce-fir forests of high elevations, while *dunni* is found in the hardwoods; the distribution of the latter is apparently correlated with the direction in which the coves face, as the salamander is found at higher elevations in the warmer coves than has been reported in the previous literature (Hairston 1947).

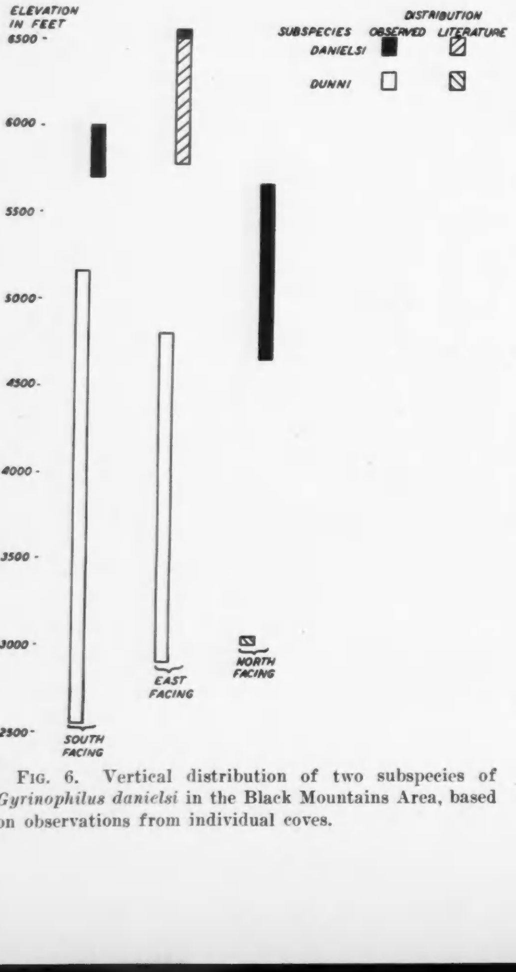

FIG. 6. Vertical distribution of two subspecies of *Gyrinophilus danielsi* in the Black Mountains Area, based on observations from individual coves.

The local distribution of the ubiquitous *Eurycea bislineata wilderae* cannot be made to fit any pattern, as it is found practically everywhere in the area. Only two specimens of *Pseudotriton ruber nitidus* were taken in the Black Mountains Area, and hence no conclusions are justified as to its local distribution.

Desmognathus is represented in the area by more species than any other genus. Furthermore, Leurognathus should really be considered along with Desmognathus in an ecological discussion, as Dunn and others have pointed out. Ecologically, it is a completely aquatic Desmognathus, and it is thought to be derived directly from *D. quadra-maculatus*, thus being genetically closer to that species than is *D. wrighti*.

If the five species representing the two genera are compared as to vertical distribution, as in Figure 2, the overlap of their ranges is more conspicuous than any differences. Plotting the distribution separately by coves (Fig. 7) only serves to emphasize the universal nature of the overlap. *D. wrighti* is nearly

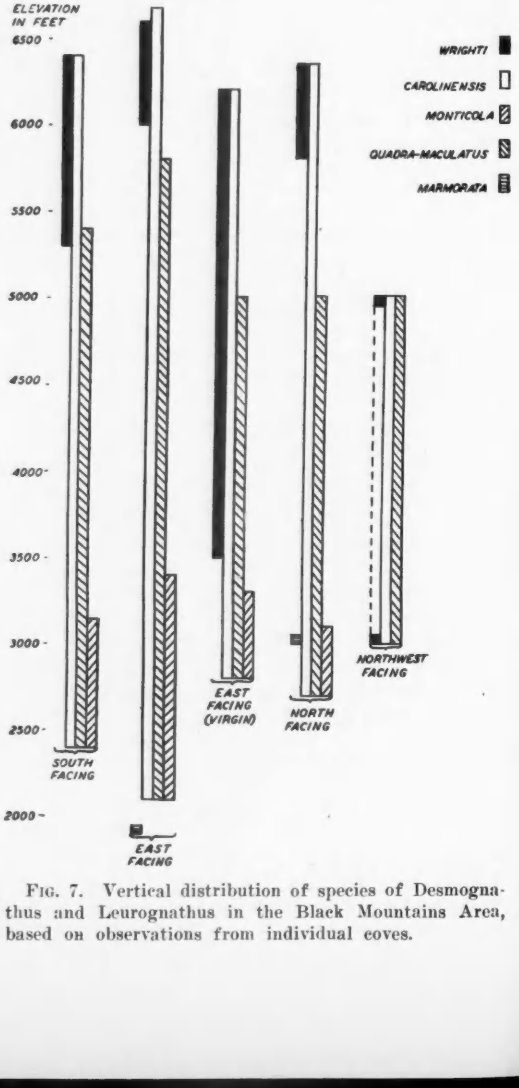

FIG. 7. Vertical distribution of species of Desmognathus and Leurognathus in the Black Mountains Area, based on observations from individual coves.

confined to the spruce-fir forest, and is certainly typical of this habitat (King 1936, 1939). Two glaring exceptions to this general rule are seen in Figure 7. The first of these, the 3,500-foot record from Middle Creek watershed, equals the recorded low altitude in King (1939), and may simply indicate that the species is able to maintain itself far down the mountainside in areas where the original vegetation has not been disturbed, and the transition from conifer to deciduous forest is gradual. The second exception is provided by two specimens taken near the headquarters of the Mount Mitchell Game Management Area in the valley of the South Toe River at an elevation of 3,000 feet. The conditions under which one of them was found show the reason for their presence. This specimen was found under a stone in a road-bed three days after the flood mentioned above under the discussion of *Plethodon yonahlossee*. Obviously, the specimen had been swept down from a higher elevation, and is not to be considered as occurring normally at 3,000 feet. The other specimen for the same elevation was taken in the adjacent woods eleven days after the flood, and the same remarks doubtless apply to it, too, although the evidence is less conclusive. I do not believe that the two specimens represent valid extensions of the vertical range of *Desmognathus wrighti*.

Desmognathus monticola has not been found above 3,400 feet in the Black Mountains Area. *D. quadramaculatus* is found up to 5,800 feet. It enters the spruce-fir forest only in Middle Creek watershed, where the conifers descend to unusually low elevations. *Leurognathus marmorata* is represented in the Black Mountains Area by only two specimens, taken at 1,900 and 3,000 feet.

Desmognathus ochrophaeus carolinensis has the greatest vertical range of any member of the genus. It has been taken from the very top of Mount Mitchell, and from the lowest location studied (Jocassee, South Carolina). The exceedingly variable color pattern of this form is well known, and has been commented on by many authors. In examining my series from the Black Mountains Area, I noticed that the specimens from the higher elevations seemed darker in color than the rest. This dark color is correlated with large size in *carolinensis* (Dunn 1926), and measurements indicated that the high-altitude specimens were somewhat larger than the remainder of the population. In order to test this preliminary observation, a large number of specimens in my own collections were measured, as well as the series in the collections of three Chicago Area museums: the Chicago Natural History Museum, the Chicago Academy of Sciences Museum, and Northwestern University Department of Zoology. In all, a total of 627 specimens were measured and the altitude whence they came recorded. When length and elevation are plotted together, an interesting picture is obtained, as is shown in Figure 8. There is a gradual but definite trend towards increasing size with increasing altitude. This trend seems clear enough, but the size range at all elevations is so great that a statistical analysis was made of the data. No obvious break occurs anywhere in the series, but it was arbitrarily decided to separate the series into two groups: those taken in or near the spruce-fir forest, and those taken in the deciduous forest. In the former group were placed all specimens from 4,500 feet or higher; the rest were placed in the second group. The mean size of the 261 specimens in the high-altitude group is 35.95±0.57 mm. for the distance from the snout to the anterior angle of the vent. For the 366 specimens in the low-altitude group, the mean length is 32.36±0.41 mm. The difference between them is significant, the ratio: difference divided by its standard error being 5.1. This observation has significance along a number of ramifications that will be discussed later.

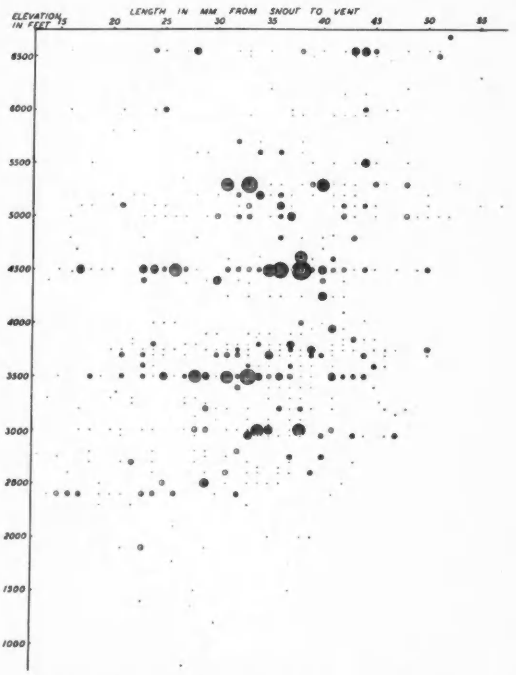

FIG. 8. *Desmognathus ochrophaeus carolinensis*: correlation of size with altitude. Circles represent additional records with identical data.

What is of interest immediately is the fact that the separation of the series into two groups was an arbitrary one. This, plus the high degree of significance, leads one to ask: what if the series had been split into three or more groups? In order to discover how many significantly different groups were present, the series was divided into three, four, five, and six vertical populations. The ratios between the mean sizes of adjacent populations and the standard errors of the differences are given in Tables 1-4. These facts are represented graphically in Figure 9. The number of populations into which the series has been divided are given on the abscissa; on the ordinate are the ratios between the mean sizes and the

standard errors of the differences for adjacent populations; the averages of these ratios are connected by a line. Superimposed on this graph are the generally accepted separations of statistical analyses. In Figure 9, the average ratio shows a clear difference for the two- and three-way divisions, and a probable difference for the four-way division, while the populations are too small to arrive at a conclusion in the cases of the five- and six-way divisions.

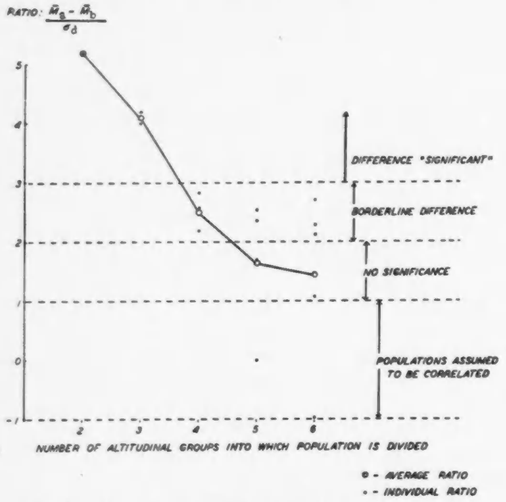

FIG. 9. *D. o. carolinensis* size cline. Differences between adjacent populations viewed as to their statistical significance. For full explanation, see text.

From the statistical analysis of the *carolinensis* series, three main facts are apparent.

1. As the subdivision of the series progresses, the average significance of the difference between adjacent groups diminishes, approximately in proportion to the number of groups.

2. As the subdivision of the series progresses, the variation in differences between adjacent populations increases.

3. The mean size of the specimens from the highest elevation is always significantly larger than the mean size of those from the lowest elevation. These three facts summarize the statistical confirmation of the original conclusion that there is a direct correlation between the size of this species and elevation collected, and that there is no point at which there is a break between the sizes of high-altitude and low-altitude specimens. In fact, the obvious conclusion is that if 6,000 specimens had been measured instead of 627, there might be as many as thirty groups, each significantly different from the adjacent groups.

The specimens from the highest elevations are separable from those from the lowest by a margin that is technically sufficient to erect a new subspecies. Approximately 75% of the adults are different as to size. But what about the intervening populations? It is clear that what we are dealing with in the present instance is a cline (Huxley 1939) and that there is no natural separation of the *carolinensis* population into two or more subspecies on the basis of altitude. It has been recommended (Dunn, in Bogert *et al.* 1943) that the opposite ends of a cline be named and the remainder of the population be treated as intergrades. While this system may work well enough at times, I believe it to be inapplicable here, since each of the various high-altitude populations in the Southern Appalachians would then become a separate subspecies, while the bulk of the species population would be intergrades.

Besides this size difference in *carolinensis*, there is a color difference that is correlated with altitude. This is the colored cheek-patch, a variant found principally in the Great Smoky Mountains. King (1939) has analyzed this character. He found that 24% of the specimens from above 5,000 feet have yellow

TABLE 1. *Desmognathus ochrophaeus carolinensis*: significance of differences between mean lengths in populations from three consecutive elevations.

Population	Altitudinal Distribution	Number of Individuals	Mean Length In mm.	Combination	Significance Ratio
a.........	5000′+	177	37.03±0.68	a vs b	4.2
b.........	3500′–4950′	277	33.63±0.47	b vs c	4.04
c.........	750′–3450′	173	30.91±0.48	a vs c	7.4

TABLE 2. *Desmognathus ochrophaeus carolinensis*: significance of differences between mean lengths in populations from four consecutive elevations.

Population	Altitudinal Distribution	Number of Individuals	Mean Length In mm.	Combination	Significance Ratio
a.........	5100′+	148	37.28±0.71	a vs b	2.53
b.........	3900′–5000′	156	35.00±0.52	b vs c	2.19
c.........	3250′–3850′	170	33.31±0.59	c vs d	2.84
d.........	750′–3200′	153	30.81±0.65	a vs d	6.7

TABLE 3. *Desmognathus ochrophaeus carolinensis*: significance of differences between mean lengths in populations from five consecutive elevations.

Population	Altitudinal Distribution	Number of Individuals	Mean Length In mm.	Combination	Significance Ratio
a.........	5200′+	126	37.37±0.84	a vs b	2.55
b.........	4500′–5100′	136	34.54±0.72	b vs c	0.00
c.........	3700′–4400′	123	34.56±0.67	c vs d	1.68
d.........	3050′–3600′	112	32.87±0.70	d vs e	2.36
e.........	750′–3000′	130	30.77±0.55	a vs e	6.6

TABLE 4. *Desmognathus ochrophaeus carolinensis*: significance of differences between mean lengths in populations from six consecutive elevations.

Population	Altitudinal Distribution	Number of Individuals	Mean Length In mm.	Combination	Significance Ratio
a.........	5500′+	79	37.72±1.09	a vs b	1.07
b.........	4600′–5400′	109	36.21±0.90	b vs c	2.12
c.........	4000′–4500′	104	33.56±0.80	c vs d	−0.99
d.........	3600′–3950′	107	34.65±0.76	d vs e	2.28
e.........	3000′–3550′	126	32.39±0.63	e vs f	2.71
f.........	750′–2950′	102	29.55±0.85	a vs f	5.9

orange, or red cheeks, whereas only 5 to 6% of the specimens from less than 3,000 feet possess the character. These figures are from the Great Smoky Mountains. The character in question has also been reported from the Nantahala Mountains (Clay and Macon Counties), the Blue Ridge (Highlands, Macon County), and from Nellie, Haywood County, all in North Carolina. An examination of 63 specimens from Highlands and immediate vicinity shows three with yellow cheeks (slightly less than 5%). Of about 300 specimens from all elevations in the Black Mountains, two specimens show some yellow on the cheek. The character is thus nearly confined to the southwestern part of the range of the species, and is apparently correlated with altitude in the Great Smoky Mountains. A second color variation in *carolinensis* is the presence of red legs, first reported by Brimley (1928) and more recently by Bishop (1947). The yellow-cheeked variety was originally given the subspecific name *imitator* by Dunn (1927) because of its striking similarity with *Plethodon jordani*. It was relegated to the synonymy of *carolinensis* by Pope (1928), who called it "an unstable color variety." The same remark doubtless holds true for the red-legged form, which parallels *Plethodon shermani* of the Nantahalas.

Mayr (1942, p. 73) has some remarks that are pertinent in this case of discontinuous variation:

"Goldschmidt and the taxonomists are probably justified in asserting that most of this variation is of minor significance in regard to speciation. The characters involved are usually not the characters which separate related species. However, Vavilov and his school have pointed out that this type of variation has some evolutionary significance, since similar mutations occurring in related species ('homologous series of mutations') give us certain clues as to the phylogeny of the germ plasm of the species involved. . . ."

Such cases "can be explained on the basis of the great phylogenetic antiquity of certain alleles" (Mayr 1942, p. 74). What is so puzzling in this double similarity to members of another genus ("homologous series of mutations") is that it occurs in approximately the appropriate areas (though less restricted in *carolinensis*) to make the parallelism complete.

The size cline in *carolinensis* is sufficiently clear to warrant an examination of the other species, especially Desmognathus, for similar trends. This type of analysis imposes conditions that are difficult to meet, namely, the species must have a large vertical range, and must be had in numbers. Of the species of Desmognathus, only *D. quadra-maculatus* approaches these conditions. If the series of this species is divided at 3,200 feet, and the two vertical groups compared statistically, the high-altitude group has a mean body length of 56.03±1.48 mm.; the specimens from 3,200 feet and lower have a mean of 51.79±1.21 mm. The ratio: difference divided by its standard error is 2.23, indicating that the difference may be significant, but that the series is not large enough to demonstrate the difference conclusively. The trend, however, is in the same direction as that shown by *carolinensis*.

None of the other species was collected in sufficient numbers to warrant a statistical analysis. *Eurycea bislineata wilderae* is the best candidate because of its great vertical range. It should be stated in this connection that *Gyrinophilus danielsi* is much larger at high elevations than at low, but that there is an abrupt change in size between the two groups, which, together with other characters, has led to the recognition of two distinct subspecies, *danielsi* and *dunni*.

HORIZONTAL DISTRIBUTION

In the introduction to his monograph, Dunn (1926) presents an account of the probable evolution of the Plethodontidae. The most complete portion of this account is the evolution of Desmognathus and Leurognathus. In these two closely allied genera, evolution is pictured as having proceeded by means of ecological, rather than geographical isolation. *D. quadra-maculatus* is visualized as the most primitive species, and differentiation has proceeded towards a completely aquatic mode of life (Leurognathus) or a nearly completely terrestrial one (*D. ochrophaeus*). Later work has only tended to increase the validity of most of Dunn's conclusions, principally through the discovery of a link between the genera (*L. intermedia*, Pope 1928) and the terminal form of the terrestrial line (*D. wrighti*, King 1936).

Without necessarily finding any descrepancies in these conclusions, the ecologist does find a number of basic problems. He would like to have an objective criterion to replace the largely subjective ones used by earlier workers ("stream vs. brook," "partly terrestrial," "banks of small streams," etc.). Partly because of the haziness of these subjective criteria, Dunn (1926, 1928) and Noble (1927), clashed over some of the points elucidated in the following discussion. Furthermore, it is desirable to know by what mechanisms ecological divergence has proceeded; i. e., exactly how do the various species that inhabit the same geographical area differ ecologically?

There is one obvious objective criterion by which we can separate species that are arranged in a progressive line from aquatic to terrestrial. This is to measure and record the distance each specimen is found from surface water, in other words, to make horizontal transects with reference to the streams. The location of 730 specimens representing the five species have been recorded in this manner. The results are given in Figure 10 and Table 5. The gradual progression from aquatic to terrestrial habitat is striking. The inclusion of *Leurognathus marmorata* on the basis of only four specimens is justifiable on the grounds that every specimen mentioned in the literature was taken from the water (Pope & Hairston 1947).

Besides the straight progression from *marmorata* through *carolinensis* toward a more terrestrial habitat, there is an increasing latitude in the type of habitat selected. The maximum concentration of in-

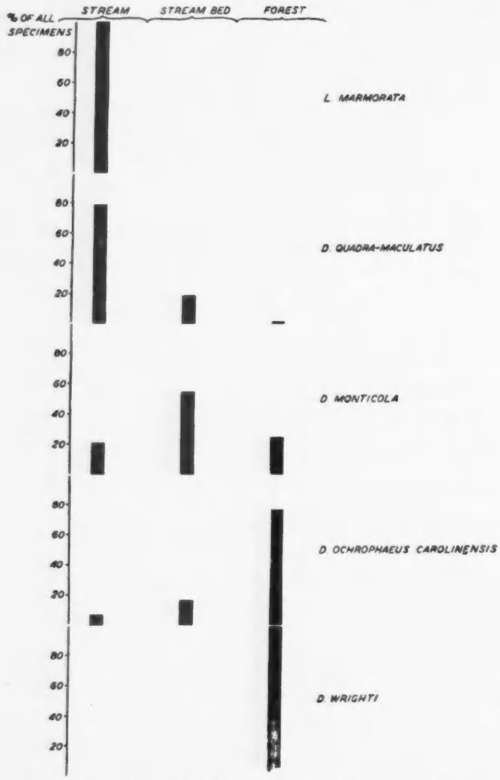

FIG. 10. Ecological distribution of the species of Leurognathus and Desmognathus.

dividuals at any point declines from 100% in *marmorata* through 78.6% *(quadra-maculatus)* and 54.4% *(monticola)* to 22.5% in *carolinensis*. Thus far up the series, the tendency towards specialization for a more terrestrial habitat[3] has not carried with it any marked tendency towards exclusion from the original aquatic mode of life. This exclusion apparently does appear in *D. wrighti*, which shuns even the vicinity of streams. Whether this is due to predation by the larger aquatic salamanders or to anatomical or physiological specialization remains to be discovered.

Another point brought out by these data is the importance of the non-inundated part of the stream bed as a distinct habitat. More *monticola* were found in this location than in all others combined. For the sake of brevity, it has been designated as "stream bed" in tables and charts, although it is, of course, only a part of the bed of the stream. This habitat is quite homogeneous, and represents an intermediate condition between the stream itself and the banks or forest. Moisture is always high, and the water is often only a few inches away vertically. Moreover, the humidity is higher over the stream bed and the temperature lower than a short distance away in the forest, as will be demonstrated below.

[3] The anatomical evidence for this specialization is discussed in Dunn (1926).

TABLE 5. Ecological preferences in the Leurognathus-Desmognathus series. Numbers in parenthesis refer to total number of specimens on which the percentages are based.

Species	Stream	Stream Bed	Number of Feet Away From Stream						
			1-10	10-20	20-40	40-60	60-100	100-200	Over 200
	Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*
L. marmorata (4)	100	0	0	0	0	0	0	0	0
D. quadramaculatus (159)	78.6	19.6	1.2	0.6	0	0	0	0	0
D. monticola (138)	21.8	54.4	19.0	4.1	0.7	0	0	0	0
D. o. carolinensis (379)	6.9	16.3	22.5	18.0	8.7	4.2	2.4	4.2	16.8
D. wrighti (50)	0	0	0	0	4.0	6.0	6.0	8.0	76.0

While the data in Table 5 and Figure 10 demonstrate the ecological divergence of the five species involved, it is less clear-cut than in the vertical distribution of *Plethodon metcalfi* and *P. glutinosus*, indicating that the various species are probably not exact ecological equivalents in their respective habitats. This must apply especially to *carolinensis* and *wrighti* in the spruce-fir forest.

There remains an analysis of the situation within one species—*Desmognathus ochrophaeus carolinensis*. Its morphological variation with respect to altitude has already been demonstrated. There is also an ecological variation. This is brought out in Table 6. It is clear that at high elevations (4,500 feet and above)

TABLE 6. *Desmognathus ochrophaeus carolinensis*: ecological distribution at high and low elevations. Numbers in parenthesis refer to total number of specimens on which the percentages are based.

Elevation	Stream	Stream Bed	Number of Feet Away From Stream						
			1-10	10-20	20-40	40-60	60-100	100-200	Over 200
	Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*
4500 ft. and higher (222)	8.6	14.0	13.5	13.1	6.8	6.8	2.6	5.3	29.3
Less than 4500 ft. (157)	4.5	19.7	35.0	24.2	12.1	1.9	1.3	1.3	0

this species is indiscriminate in its choice of habitat, while below this altitude it is bound to the vicinity of streams. Dunn (1926, p. 110) mentions this fact, but attributes the difference to a supposed intergradation with *Desmognathus fuscus* at low elevations. I do not agree that the two species intergrade (see discussion), and I am convinced that the ecological difference between the high- and low-altitude populations can be explained on the basis of environmental influences. The physical data are given in the appropriate section. In Figures 11, 12, and 13 are given the combined vertical and horizontal distributions of the species of Desmognathus in three different coves, and the difference in the distribution of *carolinensis* between the south-facing cove and the

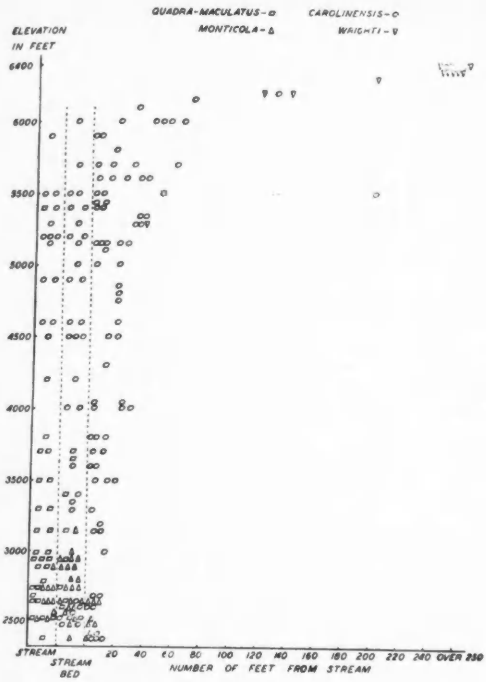

FIG. 11. Combined vertical and horizontal distributions of four species of Desmognathus in a south-facing cove (North Fork of the Swannanoa River).

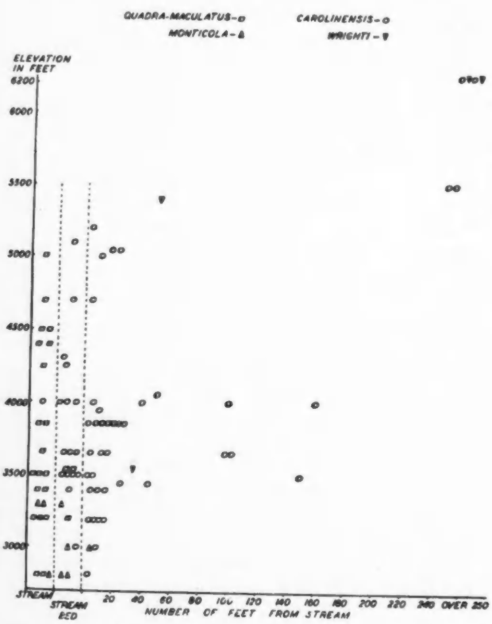

FIG. 12. Combined vertical and horizontal distributions of four species of Desmognathus in a virgin east-facing cove (Middle Creek).

other two is marked. In comparing the distribution as found in the east-facing and north-facing coves, it must be remembered that the former is virgin, while the latter is not. In the south-facing cove, *carolinensis* is confined to a zone within 40 feet of the stream at elevations below 5,500 feet. In the north-facing cove, it begins to spread out beyond this zone at 4,500 feet, while in the virgin east-facing cove the lateral spread begins at 3,500 feet.

This difference in the horizontal distribution of *carolinensis* at high and low elevations and from cove to cove parallels the situation between *Plethodon glutinous* and *P. metcalfi*, and suggests a common cause —the increase in humidity and decrease in temperature from one cove to another.

The horizontal distribution of the genera other than those already described was found to be essentially as described in the literature.

ACTIVITY OBSERVATIONS

METHOD

Activity studies were carried out at three places in the Black Mountains Area. Sugar Fork of the North Fork of the Swannanoa River enters the main stream at an elevation of 2,550 feet. A 100-yard stretch of stream and a 200-foot transect of the adjacent cove hardwoods forest were marked with paper tags so that the same route could be followed on successive trips, after the manner of Park, Lockett, & Myers (1931). Individual stations were not set up, any salamanders seen in the open anywhere along the route being recorded. This route was followed at intervals of 1½ to 2 hours over the period from 4:00 PM to 9:00 or 10:00 AM. For night observa-

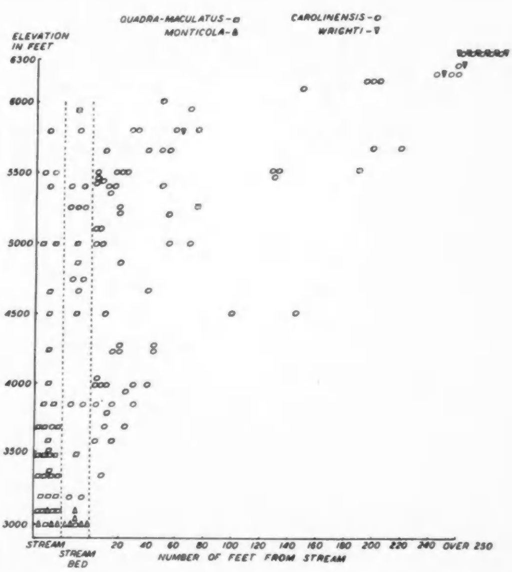

FIG. 13. Combined vertical and horizontal distributions of four species of Desmognathus in a north-facing cove (Cane River).

tions, an acetylene head lamp was found extremely useful.

The spring and adjacent spruce-fir forest near the top of Mount Mitchell were studied in the same way, except that the stream was observed only in the immediate vicinity of the spring.

The third area selected for an activity study was the spruce-fir forest at the top of Clingman's Peak.[4] Here, there is no spring, and the route followed simply formed a loop through the forest.

GENERAL OBSERVATIONS

The statement that salamanders are nocturnal will surprise no one who is at all familiar with them. Indeed, many collectors have made use of this fact in collecting and in observing habits. To this extent, the following observations are confirmatory. However, with the exception of the few observations on *Plethodon cinereus* by Park, Lockett, & Myers (1931), no previous work has included physical data or quantitative estimates, and the differences between species are new, as are the implications derived from these differences.

The method of making field observations has been described above. It was surprising how easy sight identifications were, making it unnecessary to disturb the specimens by handling them. More difficulty was encountered in deciding to what degree an individual salamander was active. Obviously, a salamander out in the open on top of a stone or on the forest floor is more active than one under a stone or log, but what if only the head of a specimen is showing? And is a salamander more active when four feet off the ground on a tree trunk than when completely exposed on the surface of the ground? In these cases, arbitrary decisions were made. Any specimen that was entirely in view was considered to be 100% active; any specimen that was still partly within its burrow was considered 50% active.

The best data obtained on salamander activity were on the four species of Desmognathus. This is because they are generally more numerous than the representatives of the other genera, and hence the data can be expressed quantitatively. In all, nine species of Plethodontidae were found active at one time or another, but of the species other than Desmognathus, only *Plethodon glutinosus* was common enough to permit a quantitative representation of its activity. This has been done in Figure 14. The species is completely nocturnal, the activity rising rapidly to a maximum at around 11:00 PM, and gradually diminishing in the early morning hours. For the other non-desmognaths, only isolated observations were made. These have been recorded in Table 7.

The activity charts of the four species of Desmognathus are given in Figures 15-17. *D. quadra-maculatus* (Fig. 15) has been observed active at all times of the day and night, but an analysis of the data indicates that it is approximately 90% nocturnal. The time between sunset and sunrise has been used as the criterion of night. In these studies, the time involved was approximately 6:30 PM to 6:30 AM, Eastern Standard Time.

FIG. 14. Activity of *Plethodon glutinosus* near Sugar Fork Creek (elevation 2550 feet).

TABLE 7. Isolated activity records of several Plethodontidae.

Species	Date	Hour	Remarks
Plethodon yonahlossee	July 28, 1947	9:10 p.m.	Nocturnal (cf. Bailey 1937)
Gyrinophilus danielsi danielsi	Sept. 12, 1947	1:00 p.m.	Specimen found active on forest floor during fairly heavy rain; if normally nocturnal, this can be reversed by weather.
Gyrinophilus danielsi dunni	July 29, 1947	3:15 a.m.	Larva in stream; subspecies presumptive, on basis of location (2550 feet el.).
Eurycea bislineata wilderae	July 13, 1947	1:45 a.m.	Apparently nocturnal; it is surprising that only one specimen of this common species was seen active.

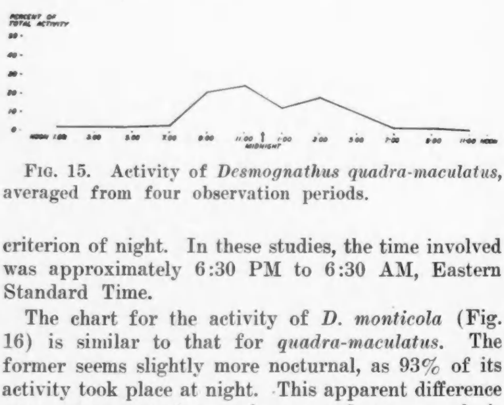

FIG. 15. Activity of *Desmognathus quadra-maculatus*, averaged from four observation periods.

The chart for the activity of *D. monticola* (Fig. 16) is similar to that for *quadra-maculatus*. The former seems slightly more nocturnal, as 93% of its activity took place at night. This apparent difference may not represent a real one, and more work is needed to establish the point. Both species are most active fairly early at night, reaching a peak at around 11:00 PM. The observations on which these charts are based were made during clear weather. *D. o. carolinensis,* though common at the same location, was only observed active once during the entire evening. The importance of its failure to appear will be seen below.

The charts of the other two species, *carolinensis* and *wrighti* (Fig. 17), show a similarity to each other in the nearly complete nocturnality exhibited: 99% for *carolinensis* and 100% for *wrighti*. The former was active throughout the night, however, while the activity of the latter was concentrated in

[4] Not to be confused with Clingman's Dome in the Great Smoky Mountains. Clingman's Peak (el. 6,593 feet) is only a few miles south of Mount Mitchell.

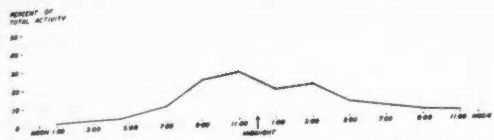

FIG. 16. Activity of *Desmognathus monticola*, averaged from four observation periods.

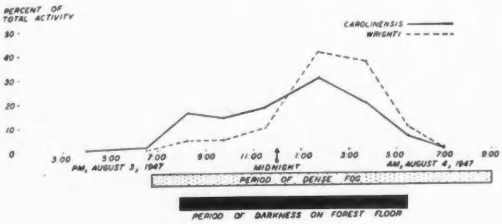

FIG. 17. Activity of *Desmognathus ochrophaeus carolinensis* and *D. wrighti* on Clingman's Peak (elevation 6593 feet).

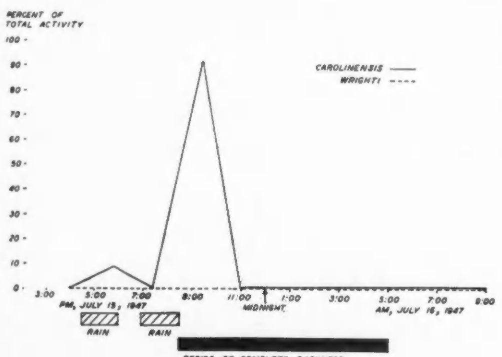

FIG. 18. Activity of *Desmognathus ochrophaeus carolinensis* and *D. wrighti* on Mount Mitchell (elevation 6550 feet). Note influence of weather; compare with Figure 17.

the early morning hours (1:00 AM to 4:00 AM). This chart represents activity on Clingman's Peak. A comparison with the data from another study on Mount Mitchell (Fig. 18) shows the importance of weather conditions in the activity of these salamanders. The weather is represented graphically on both charts. On Clingman's Peak, the mountain top was in a dense cloud all night, while on Mount Mitchell there were two thundershowers in the late afternoon, following which clear weather prevailed. The striking importance of two factors, moisture and light, is shown on these charts. In the case of *carolinensis*, the activity was distributed throughout the night when the atmosphere was saturated with fog, but was restricted to two short bursts when showers preceded a clear night. The first rain, coming late in the afternoon, stimulated some activity, even though there was still considerable light, while most of the activity took place immediately after the second shower, the end of which coincided with nightfall. The drop in humidity later on (Table 8) apparently terminated the activity although five hours of darkness followed. The coincidence of rain and afternoon hour inducing activity of both *carolinensis* and *quadra-maculatus* was observed on another occasion, while making one of the vertical transects (Middle Creek). There was no opportunity to observe the effect of rain on the activity on *D. monticola*.

Desmognathus wrighti is even more exacting in its requirements than is *carolinensis*. Although its presence was easily demonstrated on Mount Mitchell, no activity was observed under the prevailing conditions. From the evidence available, this species requires both complete darkness and a saturated atmosphere before becoming active.

The activity data permit several generalizations:

1. There is a trend from incomplete to complete nocturnality in the species of Desmognathus studied.
2. This trend parallels the progression from aquatic to terrestrial species, respectively.
3. The three species for which data are available are all affected by weather conditions in their activity. The degree of effect of a saturated atmosphere is more marked in the terrestrial species, since *quadra-maculatus* increases a tendency already present, whereas the other two need the stimulation of increased moisture to initiate their activity. *D. wrighti* in addition requires complete darkness.

The recorded physical influences of the environ-

TABLE 8. Atmospheric moisture and temperature for July 15-16, 1947; Mount Mitchell, N. C. Elevation of observations: 6550 feet.

Time	Relative Humidity (%)			Saturation Deficit (gm./cu.m.)			Air Temperature (°C)		
	Over Stream	50 ft. Away	200 ft. Away	Over Stream	50 ft. Away	200 ft. Away	Over Stream	50 ft. Away	200 ft. Away
3:40 P.M.	94			0.9			16.0		
4:00 P.M.		94			0.9			15.5	
4:15 P.M.			94			0.88			15.5
5:15 P.M.	100			0.0			11.5		
5:25 P.M.		100			0.0			11.0	
5:40 P.M.			100			0.0			11.0
7:00 P.M.	100			0.0			10.5		
7:15 P.M.		100			0.0			10.5	
7:30 P.M.			100			0.0			11.0
9:00 P.M.	97			0.4			10.0		
9:15 P.M.		97			0.4			10.5	
9:30 P.M.			94			0.7			10.5
11:00 P.M.	97			0.4			10.0		
11:15 P.M.		93			0.7			10.0	
11:30 P.M.			93			0.7			10.0
1:05 A.M.	93			0.7			10.0		
1:25 A.M.		93			0.7			9.5	
1:40 A.M.			87			1.4			10.0
3:10 A.M.	90			1.08			10.0		
3:25 A.M.		87			1.4			10.0	
3:35 A.M.			90			1.08			10.5
5:25 A.M.	90			1.08			10.0		
5:35 A.M.		94			0.75			10.0	
5:45 A.M.			97			0.35			10.5
7:40 A.M.	87			1.4			11.5		
7:50 A.M.		90			1.08			11.0	
8:00 A.M.			90			1.08			11.5

ment enhance the validity of these generalizations. They are presented in a later section.

VERTICAL MIGRATION

The activity studies led to the discovery that *Desmognathus wrighti* is almost completely arboreal during its active period, and that *D. o. carolinensis* is partly so. Specimens of both species were observed clinging to the bark of both living and dead trees in the spruce-fir forest. Figures 19 and 20 show the observed distribution of the two species through the night. Specimens not observed were assumed to be under cover on the forest floor. The number of these on each trip was arrived at by subtracting the number observed in the open at that time from the maximum number active on any trip. An additional layer has been added to the *carolinensis* chart to show those specimens that were in the entrances of their burrows.

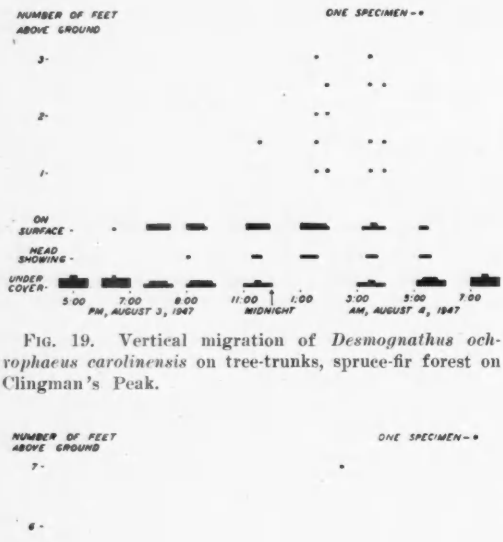

FIG. 19. Vertical migration of *Desmognathus ochrophaeus carolinensis* on tree-trunks, spruce-fir forest on Clingman's Peak.

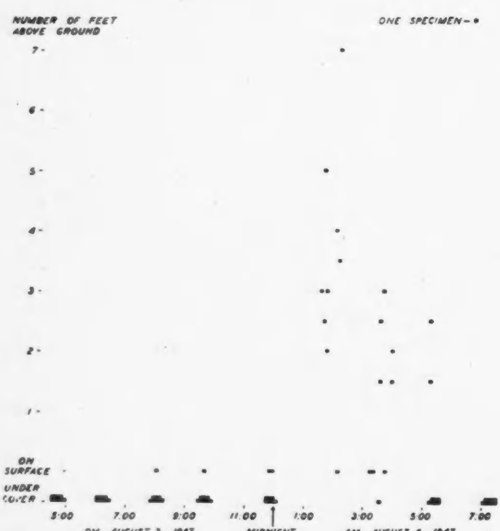

FIG. 20. Vertical migration of *Desmognathus wrighti* on tree-trunks, spruce-fir forest on Clingman's Peak.

The movement up the tree trunks was much more marked with *wrighti* than with *carolinensis;* on the trip from 1:05 AM to 2:30 AM, eight out of nine active *wrighti* were above the ground, one specimen reaching a height of seven feet above the forest floor; on the same trip, seven of thirty-two active *carolinensis* were arboreal, the highest being only three feet above the forest floor. The charts indicate a vertical migration out of the shelter niches, first to the surface of the ground and then up the tree trunks, with a return shortly before dawn. How regularly this phenomenon occurs is not known, nor is the reason for the movement. Presumably, since shelter and mating are both unlikely, search for food is involved, but this is pure conjecture. It is true that the bark of most of the trees was actually dripping water from the fog, and this water may have attracted the salamanders.

Representatives of several other genera of Plethodontidae are known to climb trees, but this I believe to be the first instance on record of a regularly arboreal Desmognathus, except for Dunn's statement that *D. quadra-maculatus* "dropped off the rhododendron branches above our heads" (Dunn 1926, p. 68). The degree of arborealism in the two species involved fits the ecological series already developed for the genus. *D. wrighti,* the terminal species of the terrestrial trend, shows a much more marked tendency to climb than does *carolinensis,* the next most terrestrial species.

PHYSICAL INFLUENCES OF THE ENVIRONMENT

METHODS

For the transects of the north- and south-facing coves, a number of physical factors were recorded. These were water, soil, and air temperatures, relative humidity, and saturation deficit. At each 500 feet of elevation, temperatures were taken of the water and of the wet sand in the non-inundated part of the stream bed, and of the air, and a sling psychrometer reading was taken over the stream. At distances of 50 and 200 feet from the stream, air and soil temperatures were recorded, as well as sling psychrometer readings. For the studies of salamander activity, the readings just described were taken during the course of each trip, except at Clingman's Peak, where one set of readings was taken outside the forest and another inside the forest, no stream being available.

The instruments used were a metal-jacketed centigrade thermometer for air and water temperatures, a Fahrenheit soil point thermometer for soil and sand temperatures, and a Taylor sling psychrometer, also reading in degrees Fahrenheit, for humidity. The saturation deficit was calculated from the psychrometer readings by the use of a Baker Nomogram. For the final record, all temperatures were converted to the centigrade scale; relative humidity is recorded in percent of saturation, and saturation deficit is recorded in grams per cubic meter.

OBSERVATIONS

In the foregoing sections, considerable mention has been made of the probable effects of climate and weather upon the distribution and activity of the salamanders under investigation. It should be realized that short-time weather data can only yield inferences as to the climate. However, any data properly taken are valid, and activity studies are not particularly concerned with long-time effects.

Continuing the general pattern of observations, the first variation of physical factors to be considered will be altitudinal differences. The most obvious difference between high and low elevations is in temperature. Chapman's Rule states that there is a drop of 1°F for each 300 feet of elevation gained. This amounts to 1°C for each 540 feet. To establish this rule, simultaneous readings at various elevations are needed. In this study, it was not possible to take such readings, but the data acquired show a general agreement with the rule, making allowances for the daily variation encountered. The best agreement with Chapman's Rule was for air and water temperatures in the transect of the North Fork of the Swannanoa River (Table 9). The figures obtained are of the same order of magnitude in the other transects, and vary from 200 ft./1°C (air temperature over Cane River) to 844 ft./1° C (soil temperature, North Fork of Swannanoa River). These figures give a general index to the applicability of the recorded temperature data. Temperature is intimately involved in the water complex, especially humidity, saturation deficit, and evaporation. These are the influences that are regarded as the most important to salamanders (Shelford 1913, 1914; Littleford, Keller, & Phillips 1947). These authors consider evaporation the most directly important of the three, but field evaporation data are much more difficult to obtain than are the others, involving cumbersome apparatus and long waits at each location. In this study, sling psychrometer readings were used, and relative humidity and saturation deficit were calculated from them. Since saturation deficit represents the drying power of the air, it is comparable to evaporation with the omission of wind, a factor much reduced inside the forest, where all of these readings were taken. A combination of factors, the principal ones being higher rainfall and lower temperature, reduces the saturation deficit at high elevations. The differences are shown in Table 10.

TABLE 9. Application of Chapman's Rule: North Fork of the Swannanoa River. For perfect fit, the figures in the right hand column should be 540 feet.

Distance From Stream	Medium	Temperature Change (°C)	Altitude Difference	Average Altitude Change/1°C
0 ft.....	Air	6.0	3000 ft.	500 ft.
50 ft.....	Air	7.5	3000 ft.	400 ft.
200 ft.....	Air	7.0	3600 ft.	514 ft.
0 ft.....	Water	5.5	3200 ft.	582 ft.

TABLE 10. Saturation deficit (in gm./cu. m.) at high and low elevations and at three distances from streams. Black Mountains, N. C., June 27-July 29, 1947.

Altitude	Distance From Stream					
	0 feet		50 feet		200 feet	
	No. Readings	Av. S.D.	No. Readings	Av. S.D.	No. Readings	Av. S.D.
4500′ +..	16	1.52	16	1.88	19	2.36
4500′ −..	28	2.37	28	2.96	27	3.11
Average		2.06		2.55		2.80

This table shows how closely correlated with moisture is the distribution of *Desmognathus ochrophaeus carolinensis* (compare with Table 6 and Figs. 11, 12, and 13). At high altitudes, the saturation deficit is the same 200 feet from the stream as it is over the stream at low altitudes. It should be emphasized that the data *do not* mean that *carolinensis* is bound to localities that have an average saturation deficit of 2.37 gm./cu. m. or less. These figures cover only one month (June 27-July 29), and the importance of the physical data presented lies not in their real values, but in their relative ones. In the late summer and autumn, it is probable that the saturation deficit is greater for both high and low elevations than the averages given here. These statements are made to avoid any possible misconception of the data. They do not detract from the clear correlation between moisture and the distribution of *carolinensis.*

A similar analysis of temperature differences shows a less striking relation to distribution. Table 11 gives the average air temperatures taken simultaneously with the saturation deficits shown in Table 10. All of the high altitude temperatures are considerably lower than the low altitude ones. The cross correlation between elevation and distance from the stream is absent. Soil and water temperatures (Table 12) show a tendency towards this cross correlation, but is not nearly as well defined as in the case of saturation deficit. The conclusion drawn from the data presented is that *D. o. carolinensis* is more closely controlled in its distribution by moisture than by temperature, although temperature may work indirectly through its relation to moisture.

The evidence is less detailed as regards the other species of Desmognathus. *D. quadra-maculatus* and *D. monticola* are not found away from the vicinity of water—good evidence for the influence of moisture upon them. *D. wrighti* is evidently limited by some factor besides moisture, since it is absent from the immediate vicinity of streams. It is significant, however, that the lowest records for this species in each cove (Figs. 11-13) are also the closest to the streams. Its absence from the immediate vicinity of streams may be due to predation by the larger aquatic species. Since *wrighti* is excluded from stream banks, its restriction to high altitudes may be due to either mois-

TABLE 11. Air temperature in relation to altitude and distance from a stream. Black Mountains, N. C., June 27-July 29, 1947.

Altitude	Average Air Temperature (°C)		
	Over Stream	50 ft. From Stream	200 ft From Stream
4500′ +	12.9	13.1	13.5
4500′ −	18.0	18.3	18.6

TABLE 12. Water temperatures in relation to altitude, and soil temperatures in relation to altitude and distance from a stream. Black Mountains, N. C., June 27-July 29, 1947.

Altitude	Average Temperature (°C)			
	Water	Soil		
		Stream Bed	50 ft. From Stream	200 ft. From Stream
4500′ +	9.3	11.2	12.7	13.0
4500′ −	15.5	16.6	17.4	18.0

ture or temperature, neither of which would be suitable for it away from streams at low elevations.

It should be stated that an attempt was made to test the relation of soil water content to salamander distribution, but no method was found to eliminate the error caused by the varying amounts of humus in the samples.

Although the humidity data are insufficient to reveal a difference between north- and south-facing coves, the temperatures presented in Figure 21 demonstrate that a difference probably exists. The overlap below 3,500 feet may be explained by the fact that the north-facing valley is under cultivation up to 3,100 feet, whereas the south-facing valley is not. The open areas permit a greater penetration of radiant energy in the cultivated zone. Data from other coves are wanting.

It is not possible to correlate the *Plethodon glutinosus-P. metcalfi* distribution with moisture in as clear fashion as was possible with *D. o. carolinensis*, since the temperature data fit the picture equally well. An examination of the ecological relationships of *glutinosus* with all of the members of the jordani (metcalfi) group on this basis would be a fruitful field for research.

With regard to the horizontal distribution of salamanders with respect to the stream, the condensed physical data have already been presented in Tables 10, 11, and 12. As the distance from the water increases, there is an increase in both temperature and saturation deficit. Experiments on the survival of three species of Desmognathus under dry conditions (Hairston, in preparation) confirm the conclusion, based on field data, that moisture is the most important physical influence operating on these salamanders. This would apply to the distribution of *Plethodon yonahlossee* as well as to the Leurognathus-Desmognathus series.

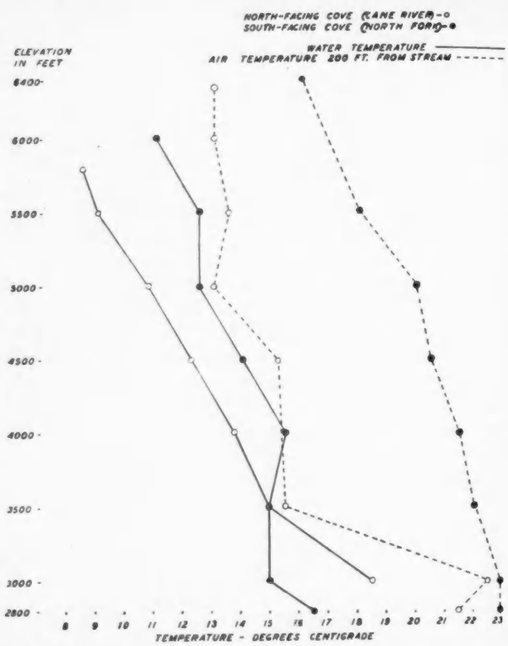

FIG. 21. Comparison of air and water temperatures in two different coves. North Fork data taken June 27-July 2; Cane River data taken July 21-24, 1947.

Some of the physical factors that influence the activity of these salamanders have already been noted in the section on activity. Since all of the observed physical influences undergo a change at night, it is difficult to decide on the basis of field observations which one or ones are the most important. Only in fortunate instances are clues available, as in the case of *D. o. carolinensis* and *D. wrighti* noted above, where the conclusion is that moisture and absence of light are the controlling factors.

The recorded physical data for the studies on activity are presented in Table 8 and Figures 22-25.

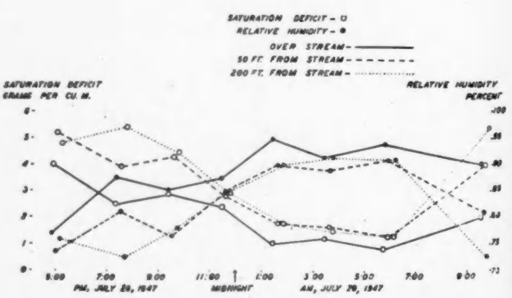

FIG. 22. Atmospheric moisture at Sugar Fork Creek (elevation 2550 feet).

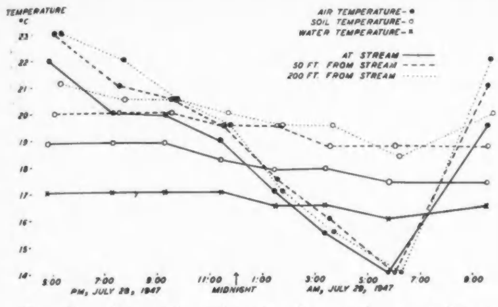

FIG. 23. Air, soil, and water temperatures at Sugar Fork Creek (elevation 2550 feet).

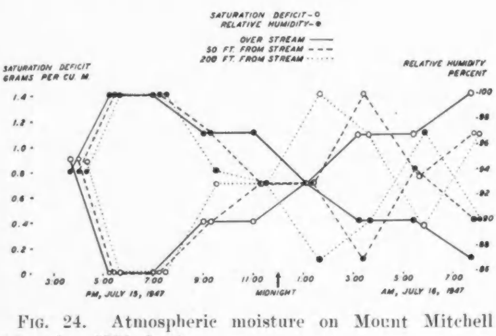

FIG. 24. Atmospheric moisture on Mount Mitchell (elevation 6550 feet).

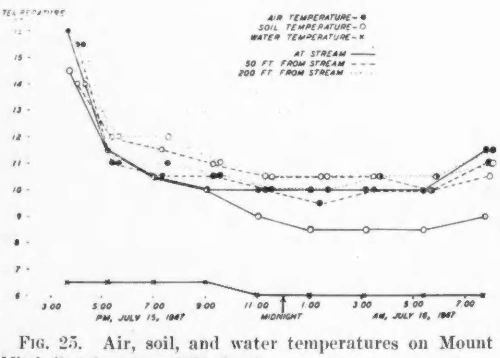

FIG. 25. Air, soil, and water temperatures on Mount Mitchell (elevation 6550 feet).

The curves follow the expected courses, with a few minor deviations. The unusual nature of the curves for the Mount Mitchell study may be explained by the prevailing weather, the two rains bringing an abrupt change to "night" conditions. One fact brought out by the data, though not surprising, is worthy of note. In the case of nearly all measurements, the fluctuation is greater away from the streams than in or near them. The importance of this fact lies in its correlation with the observed activity of the four species of Desmognathus. The greater the daily fluctuations in the physical environment to which the species is subjected, the more complete is the nocturnality exhibited. Thus *D. quadra-maculatus*, the environment of which is least variable, is 90% nocturnal, whereas *wrighti*, which is subject to the greatest fluctuations, is 100% nocturnal. The remaining species, *monticola* and *carolinensis* are intermediate in nocturnality and in the variability of their respective environments.

FOOD IN RELATION TO HABITAT

Stomach analyses were made for the four species of Desmognathus. The specimens used in this part of the study all had 95% alcohol injected into the peritoneal cavity as soon as they were killed. The stomachs were removed and cut open, and the contents sorted and identified as far as possible by Professor Orlando Park of the Department of Zoology, Northwestern University. Ten specimens of each species were examined.

The stomachs contained a wide variety of small arthropods, plus one earthworm and one snail (Table 13). For each food organism, the size and probable habitat were recorded.

There are several methods of representing the relative importance of each item of food. The one most frequently used is to record the percent of occurrence in a number of stomachs. This is a representation of one or both of two factors: availability of the prey and choice by the predator. Percent of occurrence does not show the importance to the species of salamander of each species of food, since the percentage does not represent the number of individuals eaten.

Two additional methods have been used in attempting to show the various food organisms in their relative importance. First, all of the organisms in the ten stomachs were counted, and each species rated according to its relative abundance. The difficulty with this analysis lies in the fact that all food organisms are rated equally, regardless of size. Second, the lengths of all of the food organisms were added, and each species rated, using the size factor in addition to abundance. This method, although theoretically the best of the three, has two obvious sources of error. A number of specimens were so badly chewed that they could not be measured and had to be omitted from the calculations. Since the organisms are of various shapes, length is only an approximation of size.

The results from all three methods are presented in Table 13, as each method seems to have some advantages. The results are more or less comparable. The indication is that no one item is essential to any of the four species of Desmognathus. With the exception of the Orabatidae in *D. wrighti*, no species of prey was found in more than forty percent of the stomachs examined, and these mites actually constituted only about thirty percent of the food of *wrighti*. Moreover, the exception may be explained by the known abundance and ecological importance of the Orabatidae in the coniferous forest (Jacot, 1936). All of the *D. wrighti* examined came from the conifers.

Of more interest in the present work is the probable habitat of the prey. The salamanders are ar-

TABLE 13. The food of four species of *Desmognathus* in relation to their habitat. Under "probable habitat of food," S=stream, SB=stream bed, and F=forest. Question marks under "classification" mean tentative identification; question marks under "% of total food" mean that specimens were too mutilated to be measured. "Food of unknown habitat" includes: for *D. quadra-maculatus*: Orthoptera; Diptera (Pipunculidae and miscellaneous); Coleoptera (Carabidae and Chrysomelidae). For *D. monticola*: Diptera larvae; Coleoptera (Carabidae adults and Staphylinidae larvae). For *D. o. carolinensis*: Homoptera; Diptera adults and larvae. For *D. Wrighti*: Hemiptera; Diptera; Coleoptera (Staphylinidae larvae and Chrysomelidae adults).
Plant fragments and mica, found in all four species, are not included in the table.

CLASSIFICATION OF ORGANISMS FOUND IN STOMACHS		SPECIES OF DESMOGNATHUS											
		quadra-maculatus			monticola			carolinensis			wrighti		
Order / Family / Genus and species / Stage in life history (adult unless specified)	PROBABLE HABITAT OF FOOD ORGANISMS	Incidence in ten stomachs (%)	% of total organisms in 10 stomachs	% of total food (based on length)	Incidence in ten stomachs (%)	% of total organisms in 10 stomachs	% of total food (based on length)	Incidence in ten stomachs (%)	% of total organisms in 10 stomachs	% of total food (based on length)	Incidence in ten stomachs (%)	% of total organisms in 10 stomachs	% of total food (based on length)
Plecoptera (naiad)	S	10	2.1	?									
Diptera—Dixidae (larvae)	S	20	16.6	23.7									
Dixidae or Chironomidae (larvae)	S	20	6.3	6.2									
Dixidae or Chironomidae (adults)	SB	40	10.4	?									
Coleoptera—Carabidae													
Bembidiini	SB				10	3.2	?						
Staphylinidae—*Stenus* sp.	SB				10	6.8	?						
Chrysomelidae—*Donacia* sp. (?)	SB				10	3.2	?						
Homoptera—Cercopidae	F	30	8.3	25.0									
Hymenoptera—unidentified	F	10	2.1	10.4									
Formicidae	F	10	6.2	8.3	20	29.0	?						
Diptera—Tipulidae (adults)	F	20	4.2	?	10	3.2	24.7						
Collembola	F	10	2.1	?	10	3.2	?				30	3.3	?
Araneida	F	20	4.2	?	30	9.7	?				10	0.8	0.8
Hymenoptera—Parasitic wasp	F	30	6.2	8.3				10	2.9	?	20	1.6	?
Collembola—Entomobryidae	F	10	2.1	1.4							10	0.8	0.6
Lepidoptera—Heterocera	F	20	4.2	?							10	0.8	2.5
TOTAL FOOD OF UNKNOWN HABITAT	?		25.0	16.7		15.3	20.4		33.8	3.3		10.7	11.2
Diplopoda—Julidae	F				10	3.2	?						
Polydesmidae	F				10	3.2	?						
Coleoptera—Photuridae													
Lucidota sp.	F				10	3.2	8.3						
Hymenoptera—Formicidae													
Camponotus sp. (?) (queens)	F				10	6.8	44.0						
Homoptera—Cicadellidae	F				10	6.8	?	30	11.4	16.8			
Pseudoscorpionida	F				10	3.2	2.7	10	2.9	?	40	5.0	7.5
Oligochaeta—Lumbricidae	F							10	2.9	?			
Pulmonata—Zonitidae													
Zonitoides arboreus	F							10	2.9	2.1			
Orthoptera—Locustidae	F							10	2.9	?			
Lepidoptera—Rhopalocera (larva)	F							20	5.7	41.9			
Coleoptera—Staphylinidae													
Atheta sp.	F							10	2.9	2.1			
Cisidae	F							10	2.9	2.1			
Cantharidae—*Cantharis* sp. (?)	F							10	2.9	7.3			
Diptera—Tipulidae (larvae)	F							10	2.9	13.6			
Cecidomyiidae	F							10	2.9	4.2			
Hymenoptera—Cynipidae	F							10	2.9	3.1			
Acarina—Orabatidae	F							30	14.3	2.5	90	34.7	26.4
Parasitidae	F							10	2.9	1.0	40	8.3	6.3
Thysanoptera	F										10	0.8	1.3
Collembola—Poduridae	F										20	2.5	1.9
Sminthuridae	F										30	5.0	3.8
Diptera—Mycetophilidae	F										10	17.4	30.8
Acarina—Trombidiidae	F										20	2.5	3.8
Hoplodermatidae	F										30	5.8	4.1

ranged in the table in order of increasing terrestrialism from left to right, and the prey in the same order from top to bottom. The diagonal "bar" formed by the individual columns of data indicates that there is a progression in type of food consumed, and that this progression parallels the ecological distribution of the species of Desmognathus. It is surprising to find so large a percent of terrestrial ani-

mals in the stomachs of *D. quadra-maculatus* (65%) and of *D. monticola* (75%).[5] This could be the result of two factors—flying insects falling into the water, and a stream-bank feeding niche for the salamanders. The figures for *D. o. carolinensis* and *D. wrighti*, both 100%, are more in line with expectations based on their ecological distribution.

The general relation between the size of predator and size of prey is demonstrated by the species of Desmognathus. The prey of *quadra-maculatus*, the largest species, averages 5.0 mm. in length; the prey of *monticola* and of *carolinensis* averages 4.2 mm. in each case, and *wrighti*, the smallest species, ate organisms averaging 1.1 mm. in length.

DISCUSSION

Ecological Factors in the Evolution of Desmognathus

The data presented demonstrate the value, indeed the necessity, of recording the precise location of individuals in studying ecological relationships between closely related species. Some of the misunderstanding between previous authors could have been avoided had the investigators used objective criteria in their observations, and adhered to them in their discussions. One difficulty with previous investigations has been the attempted projection of results from one area to another. The comparisons between complementary coves presented above demonstrate the dangers involved in this sort of reasoning. One observer finds a species in a "small stream," another finds it in a "muddy stream," while a third describes it as abundant in a "large clear stream." Considerable discussion arises, when it should be evident from the varying reports that the salamander is more or less indiscriminate in the type of stream selected, and that its ecological limitations must lie in another direction. These remarks apply equally well to the ecological differences between related species occupying the same geographical area. That these differences exist is scarcely to be questioned, since competition would drive out all but the best adapted form, were they identical in ecological requirements. How then do the various species of Desmognathus differ in their ecology? This question in its broadest aspects was answered by Dunn (1926). His description of a series from aquatic to terrestrial is essentially correct. The details have been challenged (Noble 1927) and defended (Dunn 1928), mostly concerning the specific ecological niches of *D. quadra-maculatus* and *D. monticola*. Most of this debate centered on the type and size of stream inhabited by the two species. The evidence indicates that both are practically indiscriminate in both regards, if observed in a sufficient number of localities. The only observed constant difference, that of direct dependence on water, is mentioned by Dunn (1926, p. 17), and emphasized by him in a later paper (1928, pp. 245-246). The results presented in this paper confirm the difference observed by Dunn in relation to surface water, but his claim that *monticola* is more or less restricted to smaller streams ("brooks") is not confirmed. The recording of the exact location of large numbers of specimens has brought out this difference between the two species much more clearly than could be done on the basis of general impressions, since the exceptions are seen in their proper proportions. Other differences in habitat preference may exist between them, but no constant ones have been found. Two coves in the same valley may differ in the relative abundance of *quadra-maculatus* and *monticola*, but an attempt to correlate the difference with differences between the streams fails in the next valley, where the situation may be exactly reversed. For example, in the valleys of the North Fork of the Swannanoa River, South Toe River, and Cane River, *monticola* seems restricted to the areas where the valleys are relatively flat and the streams slower moving (and larger!), but this does not hold on the adjacent east face of the Blue Ridge nor at Highlands, where the drop is almost precipitous and *monticola* is found in abundance.

The degree of terrestrialism, then, is the only constant habitat preference shown by the species of the Leurognathus-Desmognathus series, and it is in this light that ecological differences must be looked for. Breeding habits (Pope 1924) are of an aquatic and a semi-aquatic type, but are not safely separable beyond this rough classification.

The activity studies show differences between all four species studied. The degree of nocturnality displayed is evidently correlated with the degree of fluctuation in temperature and humidity in the habitats involved. This difference in activity pattern is further enhanced by the arboreal tendencies of *carolinensis* and *wrighti*, and here again there is a difference in degree that fits the increasing terrestrialism, *wrighti* climbing much more readily than does *carolinensis*. Incidentally, the arboreal habit represents a material extension of the adaptive radiation of the group as outlined by Dunn.

Differences between three of the species in their ability to withstand desiccation have been observed and reported elsewhere (Hairston 1947a, and in preparation). These differences demonstrate that there is a progressive difference in the physiology of the species studied (*quadra-maculatus, monticola* and *carolinensis*). The nature of the physiological mechanism involved is not known, but it is certainly worthy of investigation, since the evolution of the whole group has depended upon the increasing emancipation from the aquatic habitat.

As regards food, the differences between the species are to be viewed as effects rather than causes of the differing habitats, since salamanders will eat almost any animal that falls within the proper size range, and "No species of urodele is known to restrict

[5] An additional stomach of *quadra-maculatus* was examined as a check on these results. This (not included in Table 13) contained the following: 1 *Cyllene* adult (Coleoptera, Cerambycidae), 17 mm.; 2 Plecoptera adults, 6 and 7 mm.; 1 Plecoptera naiad, 4 mm.; 1 wasp adult, 5 mm.; 1 ant worker, 2.5 mm.; 2 winged aphids, 2 mm.; 1 muscoid fly, 9 mm.; and 1 mycetophilid fly, 3 mm. These results are consistent with the others. It should be pointed out in this connection that many fresh-water fish feed extensively on terrestrial organisms (Robertson, 1947, e.g.).

its diet to a particular kind of animal food." (Noble 1931, p. 417.)

The evolution of the terrestrial series of Desmognathus has been viewed as depending for its first step upon a physiological change involving the ability to withstand an increased amount of desiccation, as the dependence upon surface water would be the principal barrier to invasion of the stream banks. The physiological change has in each case been followed by morphological ones—more rounded and elongate tail, smaller size, loss of vomerine teeth in the male, etc. The mechanics of the original separation of the species are more difficult to visualize, since the series is in too close contact, each species with its neighbors, to suppose that the ecological separation is sufficient to isolate such a new form genetically. In other words, some sort of geographical isolation must have intervened between the adaptive steps, the ecological segregation being insufficient to account for the amount of speciation that has taken place. Dunn (1926) has outlined the probable method for the *monticola-carolinensis* pair as follows: (1) *Monticola* splits geographically into a montane form (type race) and a lowland form *(fuscus)*. (2) The isolation becomes complete, so that intergradation no longer exists. (3) *Fuscus* in typical form finds invasion of the mountains difficult because of competition with the larger *monticola;* thus the montane habitat selects for a terrestrial mode of life for *fuscus* (higher rainfall and aquatic niche blocked by *quadra-maculatus*). (4) Montane population of *fuscus*, separated geographically from lowland population, diverges as *carolinensis*, which is able to maintain itself against *monticola* by an increasingly terrestrial habit. This hypothetical series of events is sustained by the anatomical evidence, *carolinensis* being much closer to *fuscus* than to *monticola*.

Dunn seems surprised that this roundabout process was involved, as it is different from his picture of the general evolution of the group. However, there is no reason to believe that a similar series of events did not take place in each step of the increasing terrestrialism. Indeed, it is difficult to imagine the origin of each new species in the Southern Appalachians on the basis of ecological isolation alone. The difficulty lies in the fact that while they are ecologically different, they are not isolated, since in every case there is a large percentage of overlap into the typical habitat of the adjacent species. Noble (1927) theorizes that the isolation took place by separation of breeding habits, but this theory is defeated by the fact that the species whose breeding habits are known are actually closer together at this season than at any other. The fact that the details involving geographic isolation are almost incontestable in the *monticola-fuscus-carolinensis* sequence lends support to the more theoretical series described below.

In the case of the separation of *monticola* from *quadra-maculatus*, the latter is seen as diverging into a northern and a southern race, much as is now going on with *carolinensis* and *ochrophaeus*. The northern form became completely separated genetically as *monticola*, and then adjusted to the different habitat now occupied—the non-inundated part of the stream bed. The combination of genetic isolation and a different ecology allowed this species to spread over the range of *quadra-maculatus* without either form being "swamped" genetically or destroyed by competition. The only direct evidence favoring this hypothesis lies in the present geographical ranges of the two species. *D. monticola* overlaps *quadra-maculatus* completely, and occupies additional territory northward that is greater than the range of the latter. This theory is made more plausible by the present situation between *carolinensis* and *ochrophaeus*. These two are now southern and northern subspecies, respectively. It is not unlikely that *wrighti* makes the parallelism with the above theory complete. King, who described this species, says "Superficially, it resembles *D. f. ochrophaeus* most, but is not known to enter the latter's range." (King 193[illegible], p. 59.) It is not difficult to visualize *wrighti* as a dwarf form of *ochrophaeus* that has been able to enter the range of *carolinensis* by virtue of its complete terrestrialism and smaller size.

This theory of geographical divergence followed by ecological divergence and subsequent spread of one now distinct species into the range of the other, is entirely compatible with the wide occurrence of speciation by geographical variation demonstrated by Mayr (1942). Furthermore, it serves to answer a puzzling question, namely: How can genetic isolation of all of these species have occurred by ecological segregation when their habitats are mutually overlapping?

Implications of the Size Cline in Desmognathus ochrophaeus carolinensis

The demonstration of a size cline in *carolinensis* has interesting implications. The first of these is that it represents a direct application of the Bergmann Rule that cold-climate members of a species tend to be larger than warm-climate ones. The difficulty is that this rule is supposed to apply inversely in the case of poikilothermic animals, whereas here the application is direct: the high altitude (cold-climate) specimens are larger than the low altitude ones. It is true that the so-called Inverse Bergmann Rule is less widely applicable than the direct rule involving birds and mammals. In the present instance, then, some factor is evidently supravening to reverse the expected condition. Now the high altitudes in these mountains are characterized by other factors than lower temperatures. Two of these are forest type and a much greater rainfall. The difficulty with postulating that the vegetation is involved in the establishment and maintenance of size difference in *carolinensis* is that the size change is gradual, whereas the vegetational change is relatively abrupt. The general moisture conditions, however, are gradual in their change. Moreover, moisture is sufficiently important in the lives of salamanders to reverse the

effect of temperature. In this case, there exists the possibility that the sizes of the specimens represent phenotypes imposed directly by the environment, but there is no evidence favoring such a possibility. The parallel difference in the percentage of occurrence of a colored cheek is surely a genetic difference.

Two other demonstrated gradual changes in size in the amphibia are Blair's work on toads of the genus Bufo and Schmidt's on various frogs. These are gradual changes in the ratio of body-length to foot- or tibia-length. Size clines are common among birds, especially on mountainsides. Mayr (1942) points out that a gradual change is the mark of primary intergradation—evidence that geographical variation is still in its early stages, while abrupt changes between high and low altitude subspecies with a narrow zone of intergradation characterizes a secondary meeting of forms previously separated completely. The situation in *carolinensis* is clearly of the former type.

The size cline in *carolinensis* is important in one more regard. This is in the matter of its reported intergradation with *Desmognathus fuscus fuscus*. *Fuscus* is a larger, more heavy-bodied form with a keeled tail. It is characteristically a Piedmont salamander, although it has been reported from a few mountain localities. What is puzzling here is the fact that the specimens of *carolinensis* that should be most like *fuscus*, namely the low altitude ones, are actually least like that form, at least as far as size is concerned. If we accept the intergradation of the two, we are left trying to explain how the intergrades between two forms can be smaller than either, when the whole series is located along a scale of increasing elevation. Of course, a lowland subspecies connecting two mountain ones could be either smaller or larger than the other two, but that is not the situation in the present case. In the light of this evidence, it becomes of prime importance to analyze the reports of intergradation. The literature shows only three actual cases of reported intergrades. They were reported by Pope (1924), Dunn (1926), and King (1939).

Pope originally placed *carolinensis* in the species *fuscus* on the basis of habits, especially breeding habits, alone. Dunn (1926, p. 113) describing Pope's series and some specimens of his own says: "Flat Rock specimens have taken on the size, and to some extent the color and shape of tail of *carolinensis*. Brevard specimens have taken on the size and shape of tail, but not altogether the color." The Flat Rock specimens he describes (p. 19) as "almost perfect intergrades." An examination of his data on them indicates otherwise. The color of *carolinensis* is so variable that it is useless as a criterion. This leaves the size and shape of tail, both of which are like *carolinensis* "to some extent." As to how much the shape of tail is like *carolinensis*, no further information is given. The size of ten brooding adults "taken at random" averages 30.7 mm. in length from snout to posterior angle of vent, a figure that agrees perfectly with my own low altitude series, especially if the length of the vent is taken into account. They are certainly not within the size range of mature *fuscus*. King says of his series of intergrades from Big Creek, near Mt. Sterling in the Great Smoky Mountains: "The specimens in question have the keels on the tails fairly well developed, are more robust in body than is *D. f. carolinensis* generally, but approach that form in development and arrangement of pigment." (p. 561). Here we have the color character again as the only one that really bridges the gap. King has already indicated the variability of *fuscus* as follows: "The principal differences are in degree of coloration and color pattern. . . ." *Fuscus*, then, is also variable in this regard, and it seems best to consider these specimens as *fuscus*, especially as Dunn's series from Mt. Sterling appeared distinct to him, a fact that King recognized.

Thus, the evidence for intergradation between *fuscus* and *carolinensis* is poor at best, and in view of the difficulty presented by the size variation in the latter, it seems best to retain *carolinensis* as a subspecies of *ochrophaeus* as originally described (Dunn 1916).

This does not mean that *carolinensis* did not arise as a mountain form of *fuscus*. It very probably did, as noted previously, but retaining it as a subspecies of *ochrophaeus* seems to express the relationships better, since the alternative necessitates placing *ochrophaeus* as a subspecies of *fuscus*, an arrangement that creates a false impression of very close relationship. Moreover, herpetological procedure requires intergradation as a criterion of subspecies (Dunn 1934).

SUMMARY

(1) Intensive field studies have been made on the plethodont salamanders of the Southern Appalachians. The southern part of the Black Mountains of North Carolina, including Mt. Mitchell (el. 6,684 ft.), was selected as the area for most of the work, but a number of other localities were visited.

(2) The transect method was employed in determining local distribution. Eight vertical transects were made, some of them more than once. Six of these were in the Black Mountains. Short horizontal transects were made along with four of the vertical ones. These were made at 100-foot vertical intervals, and extended from the stream 200 feet into the forest. Field observations were made on the activity of a number of species, and the stomach contents of the species of Desmognathus were identified as far as feasible.

(3) The results of the vertical transects showed a striking separation of *Plethodon glutinosus* and *P. metcalfi* on the basis of altitude. Although the vertical overlap between them amounted to 1,750 feet for the whole Black Mountains Area, this was shown to be due to differing situations in different coves. *P. glutinosus* reached an elevation of 4,750 feet in a south-facing cove, but only 3,100 feet in a north-facing one. *P. metcalfi* was found as low as 3,350 feet in the north-facing cove, but only down to 5,300 feet

in the south-facing one. East-facing coves were intermediate. The maximum overlap in any cove was 200 feet.

(4) A series from aquatic to terrestrial was demonstrated for the species of the Leurognathus-Desmognathus group. This was based on data from horizontal transects in which the distance from the stream was recorded for each specimen. *L. marmorata* is completely aquatic; *D. quadra-maculatus* is 78% aquatic; *D. monticola* is characteristic of the non-inundated part of the stream bed, 54% of the specimens coming from this location; *D. ochrophaeus carolinensis* is 76% terrestrial; and *D. wrighti* is 100% terrestrial. No preference was demonstrable for a particular type of stream on the part of any of these species. *D. o. carolinensis* is restricted to the vicinity of streams at low elevations, but is distributed at random above 4,500 feet.

(5) A progression in nocturnality was found among the species of Desmognathus. *Quadra-maculatus* was found to be 90% nocturnal, *monticola* 93% nocturnal, *carolinensis* 99% nocturnal, and *wrighti* 100% nocturnal. In addition, *wrighti* is nearly completely arboreal in its activity, and *carolinensis* partly so. A vertical migration was demonstrated for both species on the trunks of trees, the maximum height attained being 7 feet above the ground for *wrighti*, and 3 feet for *carolinensis*. The activity pattern fits the series from aquatic to terrestrial.

(6) Records of temperature fit Chapman's Rule of 1°F change for each 300 feet of altitude. They further show a consistent difference between north- and south-facing coves. Saturation deficits were consistently lower at higher elevations, and at situations closer to the streams. The local distribution of *D. o. carolinensis* is correlated with atmospheric moisture, and a similar relation is thought probable for the distribution of *Plethodon metcalfi* and *P. glutinosus*.

(7) Examination of the food of the four species of Desmognathus shows that they tend to feed on animals living near their shelter-niches, but both *quadra-maculus* and *monticola* had eaten a disproportionately large number of terrestrial arthropods. The size of the food is related to the size of the salamander, but no definite ratio can be established on the basis of present evidence.

(8) Physical influences of the environment recorded during activity studies showed that those species showing the greatest degree of nocturnality were the ones subject to the greatest fluctuations in temperature and atmospheric moisture.

(9) A size cline is demonstrated for *Desmognathus ochrophaeus carolinensis*. There is a gradual increase in size with altitude. This is contrary to expectations based on the Inverse Bergmann Rule. The absence of a perceptible break in this gradual size change makes the description of a new subspecies inadvisable. The records of intergradation between *carolinensis* and *fuscus* are examined, and since they all depend primarily on color pattern, they are not regarded as valid. *Carolinensis* should remain a subspecies of *ochrophaeus*. The difficulty of explaining how intergrades between two subspecies can be smaller than either supports this conclusion.

(10) The demonstrated ecological differences between the species of Desmognathus are insufficient to account for the genetic isolation necessary to speciation as outlined by Dunn. It is probable that speciation has proceeded by geographical variation, followed by an ecological change in one species and its subsequent spread back over the geographical range of the other. That this sequence of events almost certainly took place in the *monticola-fuscus-carolinensis* series supports the theory in the less clearly demonstrable steps.

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THE RAIN SHADOW EFFECT ON THE PLANT FORMATIONS OF GUADALCANAL[1]

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[1] A dissertation submitted in partial fulfillment of the requirements for the degree of Master of Science in the University of Utah.

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THE RAIN SHADOW EFFECT ON THE PLANT FORMATIONS OF GUADALCANAL

INTRODUCTION

During the war the writer spent 22 months in the Solomon Islands, 12 of them on Guadalcanal engaged in malaria control work. The remainder of the time was spent aboard a small tanker that carried gasoline to all the occupied islands of the group. Spare time was utilized in making studies of the islands and their vegetation.

The military duties assigned while on Guadalcanal were such that from 6 to 10 hours daily were spent in the field where constant association with the vegetation made clear many factors limiting the plant types, and systematic studies of many habitats were possible. Later, after having left the island, observations were made on several other Solomon Islands thus adding to the general picture.

The writer wishes to express his thanks to Drs. W. S. Flowers, W. P. Cottam, A. M. Woodbury, and A. W. Grundman for encouragement and aid during the preparation of this paper. He also wishes to express thanks to Dr. E. D. Merrill and Dr. L. M. Perry of the Arnold Arboretum, who kindly classified most of his plant specimens and assisted him greatly in taxonomic work; to Dr. E. P. Killip, curator of the Division of Plants, U. S. National Museum, who loaned specimens from the Solomon Islands; to Mrs. Agnes Chase of the U. S. National Museum, who identified grasses; Dr. Elbert D. Thomas of the U. S. Senate who obtained maps otherwise unobtainable and to A. Herbert Gold who supplied references while the writer was in the islands.

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LOCATION, EXTENT, AND DESCRIPTION OF THE AREA

Guadalcanal is one of the southern islands of the Solomons chain and lies between 9° 15" to 9° 58" S. lattitude and 149° 36" to 160° 51" E. longitude. This places it well within the true tropic belt and the work of many plant geographers indicates that a rain forest type of vegetation should be expected. However, this island differs in having the major portion of the north coast covered with coarse grass while a true rain forest vegetation occurs only on the south portion and on the mountains. Small areas on the Florida Islands just across Iron Bottom Sound and Sealark Channel from Guadalcanal show a similar grassland while all other islands of the Solomon Islands chain are covered with forests from the beaches to the mountain tops (Ivens, 1918). Guadalcanal is unique in its position in the Solomon group in that it is the only island having its main axis running approximately east-west about 40° from the trend of the group. The main mountain ranges on the island are approximately parallel and occupy a central position. They average about 6,000 feet in elevation in the central portion of the island and Mt. Popomanasiu reaches a maximum height of 8,005 feet. Their position across the prevailing trade winds is the factor considered responsible for the grassland formation on the north coast and on the west tip of the Florida group beyond.

Local inquiries brought forth little information beyond the inference that the grasslands were the result of repeated forest fires, or results of clearing the land for agriculture. These inferences, as will be shown later, were not acceptable due to certain discrepancies. Writings of eminent plant geographers and naturalists give different interpretations of the factors responsible for grasslands in the tropics (Brown, 1919; Brass, 1938; Guppy, 1887; Lane-Poole, 1925).

Comprehensive ground studies were made only on the north coastal plain, because travel to other portions was extremely difficult, and the press of military duties prohibited any prolonged trips. It was possible to study the vegetation from the Balasuna River to Cape Esperance and to penetrate the hinterland along the Malimbu, Poha, and Tenaru Rivers to depths from 8 to 12 miles. Air trips were arranged through the courtesy of the pilots of the 13th Air Force. On these flights the entire island was covered and a far better idea of the physiognomy and extent of plant cover types was obtained.

From the air the contrast in plant cover on Guadalcanal as compared with that on other Solomon Islands is striking. A flight along the north coast of the island from east to west reveals that the eastern third of the plain is densely covered with rain forest, but the western two-thirds is covered predominantly by grass. The rivers, running through the grassland,

FIG. 1. Looking upstream on the banks of the Malimbu River. (Official Photograph, U. S. Navy.)

support strips of forest which connect the forests of the mountains with the narrow strand forest which forms a green border on the coast. The strand forest hides the grass covered plains from the shipboard observer, so that only the park-like western end is usually thought of as being grass covered.

A coastal plain makes up the major portion of the north side of the island, and extends from a point near Kau Kau Bay at the southeast to a point west of the Matanikau River where it narrows to a fringing strip which is continuous with slight exceptions to the Tenamba River near Cape Esperance at the northwest tip. This is a recently emerged coastal plain as shown by the presence of an old beach at its inland limit. This old beach still shows well preserved sea cliffs with facets still recognizable even where they were cut in unconsolidated material. The fossils in the old beach are similar to the shells on the present strand. (Kajewski, 1946). The streams on the plain are more or less parallel. There is remarkably little meandering except near the mouths where small deltas are being formed. Off shore bars are evident on the plain in a few places with depressions behind them. These depressions are usually swampy.

The eastern portion of the plain is covered with a dense forest that extends to a point west of the Kema River where it gives way to scattered grass patches. These grasslands become progressively more extensive toward the central portion of the island and, near the Berande River grass almost completely dominates the area. From the Berande River to the Lunga River the grasslands occupy all of the plains area except the narrow forest communities that border the streams from their point of emergence from the mountains to the sea. A narrow strand community of forest type borders the coast.

From the Lunga River west, the plain gradually narrows and is backed by high ridges. The grasslands occupy the slopes and tops of these parallel ridges that extend from the mountains toward the sea. The narrow coastal plain, from the Matanikau River westward, is predominantly covered with a mixed forest vegetation consisting of both strand and forest types. Some small grass areas are interspersed between the rivers. Near the upper limits of the grass on the ridges a savannah type vegetation develops, and in some places, as above Henderson Field, slope control probably determines whether grassland or savannah will predominate. None of the forest giants grow in these savannahs.

The ravines between the parallel ridges usually have a small stream at the bottom and the vegetation here is a forest type virtually identical with that of

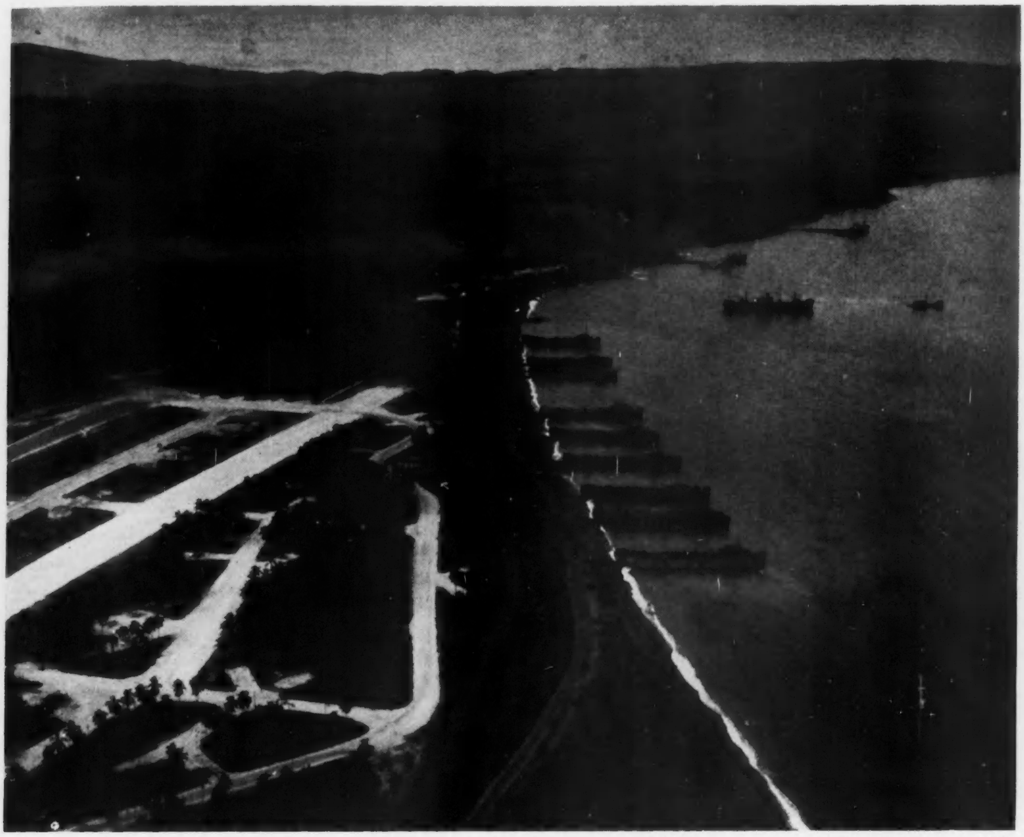


FIG. 2. A portion of the western end of Guadalcanal. Note the park-like appearance of the hillsides. (Official Photograph, U. S. Navy.)

the streamside communities on the plains, being largely made up of the same species. The ridges extend uniformly to Cape Esperance, the bold slopes of which are also covered with grass. Cape Esperance is an abrupt mountain rising sheer from the sea. It is probable that slope control exerts a marked influence here.

METHODS OF STUDY

Most of the data were collected by direct field observations augmented by the terrain maps available through Malaria Control Headquarters. Photographs were taken both in color and black and white and accurate notes kept on each.

After brief exploration to ascertain the extent of certain plant formations, detailed studies of the various communities such as strand, mangroves, streamsides, and grasslands were made. Similar communities were compared as to extent and floristic composition, effects of substrate, size of streams, salinity, flooding, topography, ground water fluctuations, and standing water.

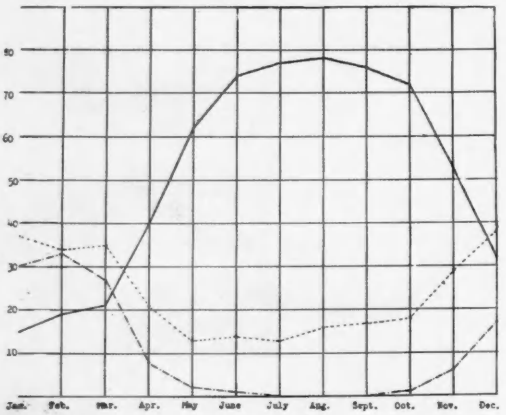
Successional studies were made in the grasslands, palm groves, and streamside communities where military operations had made necessary the removal of cover. Ground water levels or water table fluctuations were observed by noting the level of seepage in numerous deep ditches that were dug to drain areas having standing water during the rainy season. Observations were made on the levels of rivers. Wind directions, rainfall, and temperature data were obtained from the Army Air Forces Weather Division. Cloud fluctuations, both diurnal and seasonal, were studied. Effects of long drought on tropical plants, flowering of plants, distribution of epiphytes, native uses of plants, animals present, and structures of formations were also studied.

Reptiles, amphibians, insects, fish, and plants were collected, however, many of the plants were lost to the ravages of molds. Some were saved, additional collections have been borrowed, and further taxonomic studies have been made at the Arnold Arboretum. In all, a fair coverage of the occupied Solomon group and a detailed study of the north coast of Guadalcanal was made.

CLIMATE AND SEASONS

The climate of the north coast of Guadalcanal is not typical of the tropical region in which the island lies. As contrasted with other islands of the Solomon

group, the total precipitation is very low, and the seasonal distribution is unusual. No other Solomon Island has four distinct seasonal changes in weather. The average annual seasonal index[2] for Kukum is *3.6* as contrasted with Aola, *1.5* or Kieta with *1.4* (see weather chart). This climate is a product of local factors, for the Solomon Islands as a group have no dry season (Baker and Harrison, 1936), (Schimper, 1903) and the high seasonal index can be correlated with the topography and local variation of the seasonal winds. The high mountains of Guadalcanal are assumed to be responsible for the marked seasonal variation in rainfall. This idea has been advanced for other tropical areas by several workers who have studied tropical climates and vegetation (Braak, 1945; Guppy, 1887; Vischer, 1923).



S.E. ——— Calm ----- N.W. -.-.-.-.-.

FIG. 3. Wind direction graph.

The manner in which these mountains modify the climate is apparent when their roughly east-west position across the direction of the prevailing trade winds is correlated with the seasonal wind fluctuations. The dry season extends from June to August, and during this period the prevailing wind is from the southeast. The winds rise over the mountain masses of Guadalcanal losing most of their moisture (adiabatically) due to lowered temperatures as they rise. After crossing the mountains they are heated by decreasing altitude and are too dry to precipitate on the north side of the mountains. The dry leeward side thus produces a rain shadow.

During the two transitional seasons of the year, March to May and September to November, the doldrums and their intertropical fronts, which migrate north and south of the equator pass over the island causing unsettled weather. Both of these transitional periods, when the doldrums are passing over, are relatively dry thus extending the dry season to nine months at Lunga and Kukum. In 1915 only 41.7 inches of rain fell at Kukum (Pacific Islands Pilot Vol. 1, 1933), mostly during the wet season.

[2] Found by dividing the lowest monthly precipitation into the highest monthly precipitation.

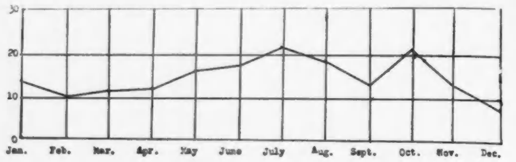


FIG. 4. Rainfall data for Kau Kau. This station receives more precipitation than other stations because the prevailing winds begin to rise here to clear the mountains. Annual average—179.63 inches.

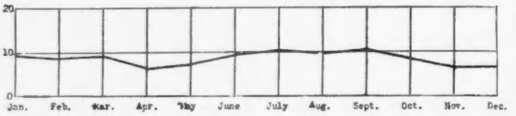


FIG. 5. Rainfall data for Aola. This station is intermediate in position between the rain shadow and the increased precipitation in the vicinity of Kau Kau. Annual average—102.21 inches.

When the intertropical front is south of Guadalcanal (December to February), the northeast trade winds cross the equator and pass over the mountain ranges of the island. During these three months over half of the total precipitation within the rain shadow occurs. This is often in the form of heavy rains that run off rapidly causing all streams to become swollen. Six inches of rain have been noted to fall in twenty-four hours.

Comparison of several Solomon Islands locations, Kieta, Tulagi, and Guadalcanal show that rainfall varies in amounts and seasonal distribution between islands and also between stations on Guadalcanal as shown at Kau Kau, Aola, Lunga, and Kukum. Kau Kau is a region of high rainfall, and a check of the topography shows that it is not in the rain shadow while Lunga and Kukum, within the rain shadow, are low rainfall areas. Kukum has 10 inches less average annual precipitation than Lunga only a few miles away. This is due to the intensity of the rain shadow cast by Mt. Popomanasiu and its sister peaks that form the highest mountain barrier rising to an elevation of 8,005 feet.

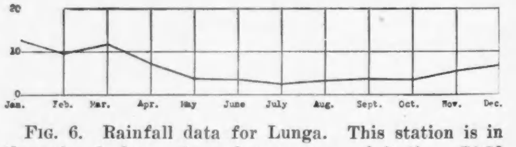


FIG. 6. Rainfall data for Lunga. This station is in the rain shadow. Annual average precipitation—74.88 inches.

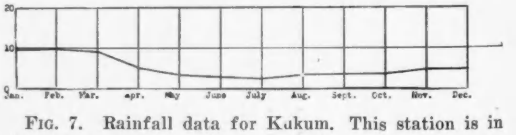


FIG. 7. Rainfall data for Kukum. This station is in the driest portion of the rain shadow. Annual average precipitation—64 inches.

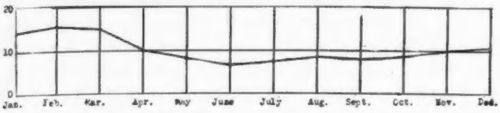


FIG. 8. Rainfall data for Tulagi. Although this station is twenty miles from Guadalcanal it is affected by the rain shadow. Annual average precipitation—123.53.

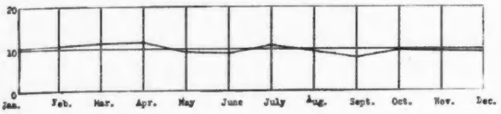


FIG. 9. Rainfall data for Kieta. This station is on the east side of Bougainville Island. The mountains of Bougainville are higher than those of Guadalcanal but are made up mainly of high, separate peaks. They are almost parallel to the direction of the prevailing winds. Annual average precipitation—119 inches.

Temperature varies very little on the plains of Guadalcanal, the annual mean being 81° F. The maximum daily temperature rarely exceeds 94° F. or falls below a minimum of 67° F. This temperature variance is not sufficient to account for any vegetational changes and it is essentially the same on all the Solomon Islands at sea level.

Humidity records are not available for Guadalcanal, but the yearly mean for Tulagi, an island only 20 miles from Lunga, is 81 percent while that of Kieta is 79 percent. Probably Guadalcanal has lower humidity in the rain shadow.

EDAPHIC CONDITIONS

While supervising the digging of numerous ditches the soil types were superficially studied. No great difference was noted between the soils of the grassland and streamside vegetation. There is a very small amount of humus under the streamside forests, but at a depth of 10 inches the red soil was the same in both situations. In some places as in meander loops and river mouths deep soil is found, but the majority of situations showed the red tropical soil only a few inches blow the surface. The strand soils are mostly sandy.

These soils are not rich in organic matter because in all tropical soils, the high rate of bacterial decay prevents accumulation of humus. The army-operated farm on Guadalcanal used commercial fertilizer extensively in order to get a favorable yield in crops. The poor condition of the soil is probably due to leaching by torrential rains, for it has been shown that areas having periodic drought in the tropics are much more fertile (Mohr, 1938). It is, therefore, apparent that lack of fertility does not acount for the grasslands on Guadalcanal. The south side of the island probably receives many times as much rain as the grasslands and should, therefore, be less fertile, but the south side of the island is covered by rain forest.

Water table fluctuations follow the seasonal rains with the expected lag. These fluctuations were observed by noting the amount of seepage in deep trenches dug through the grassland and streamside forests. During the dry season these ditches as well as many small streams were dry. A few weeks after the rainy season began seepage was noted on the banks of trenches, and the intermittent streams were all flowing. The advent of the rainy season is first felt in the mountains. Water began flowing in the small streams heading in the low mountain slopes several weeks before much rain fell on the lowlands.

During the early part of the dry season (June and July) seepage in the trenches gradually declined until only small, disconnected pools were present. The total water table fluctuation is estimated to be more than 4 feet. This amount of variation has a profound effect on the ability of plants needing large amounts of water to invade the dry grasslands, for, unless roots could penetrate beyond this depth during the wet season, they could not survive the dry season.

BIOTIC FACTORS

Time did not permit studies of soil microorganisms. At the time the study was made the cattle herds usually on the island had been entirely depleted to supplement military rations, and no effects of grazing could be seen. Wild pigs were largely confined to the streamside forests, and their rootings apparently did not effect successional changes.

Many writers have ascribed the cause of the grasslands of the tropics to fire of human origin (Braun-Blanquet, 1932; Brown, 1919; Lane-Poole, 1925; Merrill, 1914; Whitford, 1911; Kajewski, 1946). In the areas they have studied this may be true with the exception of the grasslands of parts of New Guinea and Guadalcanal which the writer believes to be climatic in origin.

On Guadalcanal no evidence was found to support the idea that constant burning of the grass was pushing back the forest. Conversely, all evidence indicates that the grassland-forest relation is relatively static and that man's activity in clearing areas for plantations is the only factor causing a retreat of the forest. As a check on the destructive power of the burned grass a section was set afire and the results observed periodically. This was done during the dry season when fire damage would presumably be most severe and while a breeze was blowing toward the streamside forest. Fire damaged the shrubs at the edge of the forest, but no apparent damage was done to the forest trees. The results showed conclusively that a fire of this intensity could not cause sufficient damage to endanger the forests, even with repeated burning. Only one fire of major size could be expected each year as the grass takes several months for regrowth.

Edges of streamside forests were checked to see if fire scars or any evidences of invasion of the grasslands by forest types could be found. Nowhere were evidences of regression of forests or grasslands found, and checking the distribution of the grasslands showed that the narrow streamside forests were a contradiction of the premise that grassland was being extended by fires. If fire were extending the

grasslands, there appears to be no adequate reason for the survival of forests along streams in the center of the greatest expanse of grass, where grass extends several miles deep at that point and the streamside forests are seldom more than 100 yards wide. The ages of burning mentioned by Kajewski *(op. cit.)* would surely have destroyed these narrow belts. The apparent age, complexity, and homogeneity of the streamside forests argue strongly against the possibility that they are regrowths replacing destroyed forests.

Further evidence that the grasslands of Guadalcanal are climatic can be shown by the presence of two species of animals both of which have been present in a suitable environment sufficiently long to become differentiated. The spotted button-quail (*Turnix maculosa salomonis*) is a small bird which is an obligate resident of the grasslands. This bird has been on the island long enough to become modified as a new subspecies. The other animal is a species of fish which has become adapted to life in the periodically dry streams, and is not found in the permanent flowing streams. This species is at present being described by Mr. Robert R. Harry at Stanford University.

The final evidence that the grassland of Guadalcanal is a climatic product is perhaps the most conclusive. Because the climate shows that a rain forest could never have grown here, any argument that it has been destroyed by fire is necessarily fallacious. It has been postulated (Lam, 1945; Schimper, 1903) that the requirements for a rain forest include a high temperature and average annual rainfall of two meters (79 inches) *distributed evenly* over the year. Although the annual average precipitation for one station on the north coast of Guadalcanal (Lunga) from 1907 to 1937 is 74.88 inches, a total too close to that of Schimper and Lam *(op. cit.)* to be significant, the distribution of this precipitation *is not even, and many years* (1915, 1928, 1930, 1935, 1941) it was less than 50 inches. These figures indicate that in all probability the north side of Guadalcanal has never supported a rain forest in the areas now occupied by grass.

It has also been estimated (Lam, 1934-35) that the rain forest requires at least 20 rainy days during the driest 4 months of the year. It is obvious from the rainfall data that this condition does not occur often. The rainfall during the dry season of Guadalcanal is mainly in the form of heavy thundershowers, which may deposit 2 inches of water in a few hours, and a total rainfall for 4 months of only 9.34 inches in 1938 and 7.73 in 1941 could well indicate that less than 20 rainy days occurred during those periods. Most of the precipitation falling in heavy thundershowers is lost to rapid runoff.

Further evidence that the grassland of Guadalcanal is climatic is shown by the difference in the vegetation on different portions of the coastal plain. That portion near Kau Kau Bay, which is a high rainfall area, is covered with rain forest. This section is not in the rain shadow for the mountains at that end of the island are too low to have any effect.

ECOLOGICAL CLASSIFICATION

The most difficult task encountered in the preparation of this paper has been the choice of terminology pertaining to the vegetation units. An attempt was made to use the classification proposed by Clements, but this system was found unsuitable in the tropics for several reasons:

1. It entirely excludes physiographic climaxes.
2. The term *association* is restricted to the climax community (Clements, 1916). This makes necessary the determination of the status of the community as to succession. This is probably impossible in a study involving a life time. For a study involving 22 months it is absolutely impossible!
3. It has as a basic concept the idea that ultimately all the land surface in a given climate will be covered with a *climatic climax* vegetation due to the reaction of the plant cover on the soil by the accumulation of humus. In the tropics oxidation and bacterial decay remove the forest litter so rapidly that no appreciable accumulation of humus can be noted.

The systems proposed by many other authors were considered (Schimper, 1903; Rechinger, 1910; Tansley, 1921; Nichols, 1923; Gleason, 1927; Egler, 1947; Cain, 1947), but no satisfactory system was found for the area under study. It was, however, apparent that any writer must define his terms carefully and strip them of the confusing conflicts borne of so many differing philosophies. The ideas of Nichols (1923) and Gleason (1927) have influenced the writer's thinking more than any others, but the classification as used in this work is a synthesis of several ideas and does not follow any one system. Any inference, however, that this is an attempt to make a new ecological classification for any area beyond Guadalcanal is emphatically denied.

According to Nichols (1923) any system of ecological classification to be complete must consider the three basic factors involved in the environment, that is, climate, physiography, and biota. Gleason (1927) adds that the biotic factors must be examined from the historic perspective in order fully to understand the problem. These ideas are in agreement with the observations made by the writer, so the following classification is used as here defined:

1. Plant formation: A complex of associations in which one of the three basic factors of the environment exerts a demonstrable control. Accordingly, three types should be distinguished, Climatic, Physiographic, and Biotic. The latter is not definable on Guadalcanal, but the short grass prairies of the midwest states in the United States or similarly heavily grazed areas of Africa might serve as examples. The formations remaining are climatic and physiographic, but, since the controlling factor in the physiographic formation is saline soil, the formation is termed *edaphic*.

2. Belt: A general term for the parallel groups of

communities of different types altitudinally distributed one above the other on mountains.

3. Association: A plant community of relatively uniform physiognomy and floristics that can be reasonably well defined in the field. No attempt is made to establish its successional rank. However, it is used in both the concrete and abstract senses. The idea that the association is an "organism" (Clements, 1916) or "quasi-organism" (Tansley, 1921) is *not* implied.

4. Community: An ecological plant structure of unrecognized rank.

VEGETATION UNITS

The natural plant communities of Guadalcanal can be grouped under three formations, that is; a strand formation, a tropical forest formation, and a grassland formation. These formations contain the following units:

1. Strand formation.

a. Terminalia-Calophyllum association. The strand community found on the sandy shores.

b. Barringtonia-Calophyllum association. The strand community found on rocky or gravel shores.

c. Mangrove association. The strand vegetation of mud flats and lagoons.

2. Tropical forest formation.

a. Lowland forest belt. The forest associations of the sea level plain and mountain slopes and of that portion of the plain not in the rain shadow. Usually below 400 feet.

(1) Streamside communities. (No definite dominants). The various communities bordering the streams that flow through the grasslands.

(2) Lowland forest associations. Communities of the plains not in the rain shadow and the lower slopes.

b. Mid-mountain forest belt. The forest associations of the mountain slopes, usually found above 600 feet and reaching 3,000 feet on exposed slopes.

c. Upland forest belt. Plant communities of the higher mountains generally above 3,000 feet.

3. Grassland formation.

a. Themeda association.

b. Themeda-Phragmites association.

It is probable that many other communities could be segregated with further study.

The lowland forest associations and the upland forest associations were not studied in detail and so, will be discussed only summarily. It is pertinent to note that Kajewski *(op. cit.)* suggests that even the upland forests in the vicinity of Mt. Tatuve on Guadalcanal are not as luxurious as those on Bougainville at similar altitudes. This is in accord with the rain shadow effect idea.

Many large plantations have supplanted the native types along the coast, and these will be briefly discussed.

STRAND FORMATION

TERMINALIA-CALOPHYLLUM ASSOCIATION

The sand association occupies the greater portion of the strand, and, with the exception of the mouths of streams, is continuous from Kau Kau Bay to Kukum point with scattered portions beyond this point. It presents a remarkably narrow strip of dark green vegetation dominated by trees about 60 feet high with a scattered undergrowth of shrubs and herbs. In many places it is less than five yards wide.

This association has a layered structure and grows only a foot or two above high tide line. The waves often break on the boles of some trees. At high tide there is almost no beach visible, and at low tide only a narrow beach is exposed.

The dominants are all medium to large trees:

1. *Terminalia catappa* L. (A large tree with large obovate leaves clustered at the ends of branches).

2. *Calophyllum inophyllum* L. (A heavy boled tree sixty feet high with shiny leaves and fragrant white flowers).

3. *Cebera Manghas* L. (A strand tree of considerable size which has white flowers and purple fruits the size and shape of a hen's egg).

4. *Cocos nucifera* L. (The coconut palm).

5. *Heritiera littoralis* Dry.

6. *Pongamia pinnata* (L.) Pierre.

Barringtonia asiatica (L.) Kurz is occasional. The giant *Ficus* common in the rocky western portion of the strand is absent from sandy areas. Many other typical strand trees are mixed with the listed dominants.

The shrubby layer is mainly made up of *Hibiscus tilliaceus* L., *Pandanus tectorius* Murt., *Guetarda speciosa* L., *Thespesia populnea* (L.) Sol., and *Desmodium umbellatum* (L.) DC.

An herbaceous ground layer composed of the following plants is present under the shrubby larger plants: *Ipomoea pes caprae* (L.) Roth., *Emilia sonchifolia* (L.) DC., *Euphorbia hirta* L., *Triumfetta bartramia* L., *Wedelia biflora* (L.) DC., *Canavalia maritima* (Auble.) Thouars., and *Momordica charantia* L.

The last two plants make up tangles in the shrubs and trail among the grasses, sedges and other low plants of this area. Occasional large lianes *(Celastraceae)* are seen and the climbing aeroid *(Rhaphidophora)* is encountered in denser stands.

The strand association within the rain shadow is generally poor; it is lacking in depth, the larger trees are reduced in size, and many epiphytes and tree species are entirely lacking. There is no gradual transition inland to a forest type as is the case in most other strand associations. The strand elements give way abruptly to the rank grass *(Themeda triandra*, Forsk) which often extends an unbroken steppe to the bases of the mountains several miles inland. This abrupt termination of the strand association is observable only along the coast which is in the center of the rain shadow. East of the Berande

River a gradual transition to a forest type is the usual condition.

Another striking difference from ordinary strand vegetation is the scarcity of epiphytes in this narrow strand association. Ferns are few in number and only a few rank orchids make up the epiphytic flora. This paucity of epiphytes is attributed to the very low rainfall in this region, and to the drying effect of land breezes on this association as they come off the grassland during the dry season. The humid sea breezes could hardly be expected to compensate for the low precipitation.

It is pertinent to note here that the trees on the edges of small lagoons formed at the mouths of streams are clothed with epiphytes overhanging the water. The presence of water below would certainly increase the amount of humidity in the air immediately above, and two benefits would accrue to the overhanging epiphytes, that is, a reduction of transpiration rate and more water available to the air roots. This condition is considered as evidence that the epiphytic flora of the strand association within the rain shadow is limited by lack of available water. The floristics of the strand association on sandy areas is noticeably different from that of the rocky areas to be described below.

In several places in the area between the mouth of the Lunga and Tenaru Rivers the typical strand vegetation has been removed and groves of coconut palms have been planted. In some places scattered patches of *Hibiscus tilliaceus* are becoming established.

Where no disturbance by man has occurred the character of the *Terminalia-Calophyllum* association is noticeably different in the rain shadow area from the strand associations in other parts of the islands.

BARRINGTONIA-CALOPHYLLUM ASSOCIATION

Westward from Kukum point the strand is composed of solid coral limestone topped with a sandy soil or very coarse gravel. The coral limestone is newly elevated sea coast while presence of the gravel is due to the steep gradient of the streams behind the strand and to a marked westward sea current which prevents the formation of deltas at the mouths of streams by removing fine sands and sediments and leaving the coarse materials on the beach. Good deep soil is present behind the strand and supports a forest of different character to that on the strand proper.

The dominants on the rocky strand vary markedly with differences in substrate. *Calophyllum inophyllum* L. and *Barringtonia asiatica* form almost pure stands on the coral rock areas, but are mixed with other strand elements elsewhere. On the gravel areas a mixed littoral forest is typical with no one tree species predominating, although *Calophyllum* approaches dominance. The huge banyans (*Ficus* sp.) are scattered in the strand often at the water's edge, grim monuments to strand trees strangled by their numerous aerial roots. These banyans are among the largest trees of the area, exceeding 120 feet in height, and are exceeded in height only by the giant forest trees back of the strand. This portion of the strand association is also layered.

Other tree species common to this part of the strand are: *Cocos nucifera* L., *Terminalia catappa* L., *Erythrina variegata* L. (*E. indica* Lam), *Parinarium* sp., and *Hernandia ovigera* L.

Many small trees and shrubs make up a second layer. Among these are: *Thespesia populnea* (L.) Sol., *Hibiscus tilliaceus* L., *Pandanus* sp., *Premna integrifolia* L., *Scaevola frutescens* (Mill.) Krause, *Tournefortia argentea* L., *Guetarda speciosa* L., and *Casuarina equisetifolia* L.

Many *Rhaphidophora* and other aeroid climbers are to be observed, and occasional lianes such as *Mucuna brachycarpa* Rich., *M. gigantea* DC., *M. elegans* Merr. and Perry, and *Derris trifoliata* Lour. drape the inland edge of the forest.

Herbs and grasses grow luxuriantly here, the herbs being mostly trailing or climbing types such as *Ipomoea pes caprae* (L.) Roth., *Vigna marina* (Burm.) Merr., *Borreria articularis* (L.) F. N. Will., *Canavallia maritima* (Aubl.) Thouars., and *Ipomoea gracillis* R. Br.

Weeds such as *Emilia sonchifolia* (L.) DC. and *Wedelia biflora* (L.) DC. are abundant.

The prevalent grasses are *Digitaria microbachne* (Presl.) Heur., *Panicum reptans* L., and *Eragrostis amabilis* (L.) Hook and Arn. Several other less common grasses are also found here. These plants together with many small trees, shrubs, and vines often form a tangled and interwoven growth that is nearly impenetrable. These tangles are scattered, however, not making a barrier comparable to that encountered at the edges of streamside communities.

Some of the many epiphytes found in this portion of the strand association are listed below and their niches noted. The "ant plant" (*Myrmecodia Muelleri* Bl.) s prominent in this area being most numerous on *Barringtonia asiatica* especially where the tree leans over the ocean. In several places ant-plant communities were noted where *Myrmecodia*, *Hydnophytum*, and *Polypodium sinuosum* Wall. were numerous on *Barringtonia* and *Calophyllum* almost to the exclusion of other epiphytes. Disturbance of any one of these plants brings forth thousands of tiny stinging ants from the modified stems where they live in symbiosis with the plants, the plants giving shelter and the ants protection from molestation. Ant-plant communities were noted in several places in the trees of this area and were the only places where all three ant plants were found together.

The ferns, *Polypodium punctuatum* Sw., *Drynaria quercifolia* L., *Asplenium macrophyllum* Sw., and *Cyclophorus lanceolatus* (L.) Alston, are found in abundance on the rough bark of *Calophyllum inophyllum* and seemingly always restricted to the inland side of the tree away from the salt spray. *Asplenium macrophyllum* Sw. is usually found high in the trees while the others are lower on the boles and low branches.

Orchids, as represented by *Dendrobium veratrifo-*

lium Lindl, *Sarchochilus moorei* (Rchb. f.) Schltr., and *Dendrobium hispidum* A. Rich., are present in abundance. *D. veratrifolium* is the commonest orchid of the entire coast. It is usually found on the trees overhanging the ocean, on horizontal limbs and dead projections from the crown. *Sarchochilus moorei* is quite rare, but inhabits less exposed situations, and *Dendrobium hispidum* clothes the inland sides of the leaning strand trees, principally on the rough bark of *Calophyllum inophyllum*. It also forms dense mats on the upper surfaces of horizontal limbs in shade where it is almost always associated with *Polypodium punctuatum*. These tiny orchids seem to flower all together in May, and the resulting tiny white and lavender blooms achieve an effect far more striking than one would expect. There are several factors responsible for the abundance of epiphytes in this area, one of which is the fact that many of the strand trees, being securely anchored in the coral substrate, lean out over the ocean, often being nearly parallel to the surface of the water and only a few feet above it at high tide. The increased humidity immediately above the water is thus available to epiphytes on these trees.

This portion of the island is subjected to the maximum effect of the rain shadow and receives 10 inches less average annual precipitation than the portion of the strand east of Lunga point. A line drawn across the island in the direction of the prevailing winds passes through the Mt. Popomanasiu crest and also through the middle of this strand forest. The high (8,005 ft.) mountain is the most significant factor responsible for the lowered rainfall in the area under discussion. The fact that the grassland reaches its maximum altitudinal range on the ridges behind this area is also evidence that this is the area most affected by the rain shadow. In the light of these facts the presence of a comparatively luxuriant strand epiphyte vegetation must be explained on the premise that more water is available from sources other than direct rainfall. Many small streams traverse the area producing standing water behind beach bars and provide more available ground water while denser vegetation decreases wind velocities. Here, also, epiphytes are most numerous near and above the standing water behind beach bars at stream mouths.

THE MANGROVE ASSOCIATION

Mangroves are found at the mouths of the large, relatively mature streams that are forming limited deltas, and in the lower reaches of small, intermittent stream courses where beach bars dam the stream mouth except for periodic flooding by tides. All areas where mangroves are found are brackish to a certain degree and different mangrove species tolerate different amounts of salinity and are arranged accordingly in definite tolerance zones. Seen from a distance, they blend into the forest type behind them, and do not give a definite line of demarcation. From close range the dense stands of trees form a canopy of shiny leaves under which an undergrowth is lacking. Prop roots extend down from trunks and branches and masses of breathing roots arise vertically from the mud and water.

The two dominant mangroves, *Rhizophora mucronata* Lam and *Brugiera conjugata* (L.) Merr. have prop roots which arch into the mud and water. These roots make travel on foot in the mangrove swamps almost impossible. Both of these trees have seeds that germinate on the tree and produce long roots which stand upright in the mud when finally dropped. This adaptation solves the problem of germination in this unfavorable environment.

Brugiera sexangula (Lour.) Poir. is a common mangrove of the Guadalcanal coast, and is found in small tracts at the mouths of the large rivers. This tree often reaches a height of 60 feet or more in favorable places, but is generally smaller. It is better able to tolerate fresh water than is *Rhizophora mucronata* and is always found behind the latter with respect to the ocean front. The segregation of these two mangroves is well shown on the Kirigi River leading into Purvis Bay in the Florida group where *Rhizophora* forms extensive coastal belts, while *Brugiera sexangula* is confined to the stream mouths where the water is less saline.

Xylocarpus granatum Koenig. is another tree often found in mangrove communities, but is less tolerant of salt than is *B. sexangula*. It is a large spreading tree characterized principally by its large green fruits. This tree is never found on the ocean front, but is confined to the less saline inland areas. Still farther inland the Nipa palm (*Nipa fruticans* Thunb.) forms small stands in the least saline waters behind all the other mangrove elements. This attractive palm is not found in extensive stands anywhere on Guadalcanal, but is restricted to the mouths of small intermittent streams that become brackish as tide water enters them. The stems are short and massive, barely rising above the water, and arising from them are large pinnately compound fronds eight to ten feet long. Growing near the *Nipa* is *Sonneratia lanceolata* Bl., a small mangrove, characterized by small, lanceolate leaves and erect breather roots. Trees of the strand and streamside appear along the edges of the mangrove stands. Among these are *Cerbera manghas*, *Calophyllum* sp., *Barringtonia racemosa* (L.) Blume, and *Brownlowia argentata* Kurz. Many others occupy the slightly raised areas that salt water does not reach.

Rhizophora mucronata is the commonest mangrove of the Solomon Islands, but is the least common on Guadalcanal. It tolerates a higher salinity than other species and this factor apparently controls its distribution. It does not grow well in the areas of fresh water as shown by its absence in the swamps behind beach bars and at the mouths of large rivers. Most of the coast of Guadalcanal is too sandy for its growth. As a result, only a few of these low, prop-rooted trees are seen, and these mainly at the mouths of the Tenaru, Malimbu, and Lunga Rivers on mud flats that are under salt water at high tide and supplied with fresh water only during the short rainy season.

Also found here is *Acrostichum aureum* L. a large fern with great leathery fronds reaching 5 feet in length. It grows mainly in or near the mangrove swamps. On the borders of the swamps the following are found: *Cycas circinalis* L., *Scirpodendron ghaeri* (Gaertn.) Merr., *Premna* sp., *Dianella ensifolia* (L.) DC., *Cyperus umbellatus* Naves, *Fimbristylis diphylla* Vahl., *Wedelia biflora* (L.) DC., species of *Zingiberaceae*, grasses, and many others.

Epiphytes are virtually absent on the mangroves except in protected places where the trees are covered with mosses, small ferns, ant plants, and grass-like orchids. The larger orchids and ferns are mostly absent from the true mangroves, but are numerous on the trees bordering the swamps and especially so on the horizontal branches overhanging the water. Among these epiphytes are: *Myrmecodia salomonensis* Becc., *Hydnophytum* sp., *Hoya* sp., *Hoya imbricata* Dcne., *Dendrobium veratrifolium* Lindl., *Polypodium punctuatum* Sw., and *Davallia* sp.

Mangroves do not invade the beaches on the north coast of Guadalcanal as they do in the bays of the Florida Islands and many other protected bays in the Solomon Island group. Their absence from the coast is attributed to the nature of the ocean front which is exposed to waves and strong currents, and is usually too sandy to offer a substrate sufficiently stable for the plants to establish themselves.

The mangrove associations are not greatly affected by the rain shadow except to the extent that the intermittent streams are flooded by tide water making the habitat more suitable for their growth.

SAGO SWAMPS

True sago swamps of the size and composition seen in New Guinea are not found on Guadalcanal. Some mixed stands of *Metroxylon solomonense* (Warb.) Becc. were observed in the oxbows on the deltas of large streams, and an occasional sago palm is often seen in the isolated oxbow communities found in the grasslands east of the Malimbu River.

TROPICAL FOREST FORMATION

LOWLAND FOREST BELT

Streamside Communities

The most striking feature of this community is its abruptness, often rising directly to a height of 150 feet above the grassland with little or no transitional belt. This abrupt rise gives the effect of a wall of vegetation when seen from the grasslands. From the air these belts of streamside forest are dark strips of green running parallel to each other across the yellow-green grassland.

No single tree species dominates the vegetation of the streamsides with the exception of a few localized areas where one species may predominate. The community is made up mainly of lowland forest types and some strand elements that do not require salt, but is quite different from the forests on the mountain slopes, and areas beyond the rain shadow.

Along each stream the communities differ widely in structure, density, and depth. The greatest difference, is between vegetation bordering temporarily dry streams and that bordering constant streams. This difference is mainly in depth. The streamside vegetation increases in height with the width and constancy of the stream. However, this general rule does not apply where large, constant streams have cut deep channels with vertical banks rising abruptly from the water. These places are almost devoid of streamside trees, the grass extending to the banks of the stream. The Tenaru River shows this discontinuity of the streamside forest about two miles inland from its mouth. This condition is due to the depth of ground water during the dry season. Parallel conditions are seen along streams in the arid western United States.

FIG. 10. The streamside community as it appears from the grassland. Notice the even canopy as contrasted with Figure 11. This vegetation is along a permanent stream.

Many of the smaller streams crossing the steppes become temporarily dry and have a continuous bordering belt of vegetation of tree species that are usually smaller than those along the constant streams. Occasionally a forest giant standing alone overtops them by many feet, and gives a ragged appearance to the forest canopy as contrasted with the even wall of forest along the constant streams. (See Fig. 11). Some of the temporary streams have flowing water for such short periods that the bordering forest is absent with the exception of oxbows where water stands after rains. These small streams often show a strand or mangrove type of vegetation near the sea, where tidewater keeps a short section of the channel full of water. Inland, these local stands give way to coarse grasses *(Sacharum)* and to small savannahs of *Pandanus* which are restricted to the banks of the water courses or to small depressions within the grassland formed by old beach bars, and never invade the grassland.

A study of the streamside communities reveals certain strata that can be fairly well defined and delimited. These strata approach the complexity reported for other tropical areas (Schimper, 1903). Here, too the effect of ground water seeping laterally from the stream supply is shown. The number of

FIG. 11. The vegetation bordering an intermittent stream. Notice the ragged appearance of the canopy.

recognizable strata is directly proportional to the size and constancy of the stream. Some of the larger rivers have several recognizable strata, while smaller streams have less, and some are represented by a single stratum. The composition of the vegetation along some of the large permanent rivers (Malimbu, Tenaru, Berande, Lunga) is nearly as complex as that of the forests of the lower mountain slopes and is often indistinguishable from it. It is along the smaller streams that climatic extremes reflect greatest changes.

The strata may be conveniently divided into:

1. Ground layer: plants covering the ground and seldom more than 3 feet in height.

2. Shrub-small-tree layer: woody or herbaceous plants more than 3 feet in height and not exceeding 30 feet.

3. Secondary forest tree layer: trees over 30 feet and usually not over 80 feet in height.

4. Primary forest tree layer: The largest trees of the forest which overtop the secondary forest trees and often reach 150 feet in height.

All these strata are present only in the communities bordering constant streams. The secondary forest layer is the top stratum along streams having only short periods of dryness. Tree types are absent along water courses that are dry for long periods.

The ground layer is often absent in the interior of some dense stands due to insufficient light. In these shaded areas only trunks of large trees, contorted lianes sprawled on the ground, low fan palms, and a few broadleaved herbs are seen. Where sufficient light penetrates, the following plants are found in abundance: *Nephrolepsis biserrata* Schott. (A fern), *Lygodium* sp. (A climbing or trailing fern), *Dryopteris* sp., *Selaginella caudata* (Desv.) Spring., *Vernonia cinerea* (L.) Less. (A weedy compositae found in the angles of buttressed trunks), *Centotheca latifolia* (Osb.) Trin. (A common grass of the stream banks), *Digitaria microbachne* (Presl.) Heur. (A low grass), *Pennesetum macrostachyum* (Brogn.) Trin., *Oplismenus compositus* (L.) Beauv. (A very large grass found in local patches where a forest tree has fallen, or on the edges of the forest), *Colocasia esculenta* (L.) Schott. (The taro plant), *Tacca pinnatifida*, Forst. (A low, pinnate leaved herb), and *Ipomoea batatas* (L.) Poir. (The yam vine).

In addition to its position as the lowest stratum the ground layer plants have a lateral distribution in the streamside forest which is controlled by shade. These plants are most numerous a few feet from the edge of the grassland or stream where the proper intensity of light gives optimum conditions.

The shrub-small-tree layer is confined to the outer edges of the streamside vegetation either along the stream banks or facing the grassland. The plants of this layer do not tolerate the extreme shade inside the streamside forest, so this stratum is more nearly a horizontal structure than a vertical one. This layer is composed mainly of woody plants, but some of the herbaceous types are so large that they also belong in this stratum. On Guadalcanal these plants make up a large portion of the vegetation along the forest edges. Such plants as the elephant-ear plant (*Alocasia macrorhiza* (L.)) Schott., wild ginger (*Costus sericeus* Bl.), banana (*Musa paradisiaca* L., *Musa* sp.), papaya (*Carica papaya* L.), and castor bean (*Ricinus communis* L.) are in this group.

The Bamboo (*Schizostachyum* sp.) when present is always found on or very near the stream banks where it forms impenetrable thickets. The wild banana *(Musa)*, the fish tail palm *(Caryota)*, the Betel nut palms (*Areca* spp.) and the castor bean plant also inhabit the edges of the streams. The latter species grows especially well on the areas denuded by floods where it often reaches 20 feet in height. *Carica papaya* L. also inhabits stream banks where ample light and water are available. *Alocasia macrorhiza*, *Costus sericeus*, and *Globba marantina* L., conversely, are more numerous near the outer borders and in small clearings.

Clerodendron buchanani (Roxb.) Walp. prefers the more shaded areas and is often abundant, but most of the other shrubs and small trees prefer more sun.

The following are some of the plants found in the shrub-small-tree layer: *Hibiscus tilliaceus* L., *Pipturus incanus* (Bl.) Wedd., *Pandanus* sp., *Morinda citrifolia* L., *Kleinhofia hispida* L., *Macaranga tanarius* (L.) Muell., *Trema aspera* Bl., *Uncaria* sp., *Melochia indica* A. Gray, *Solanum aff. vitiensis* Seem., *Breynia* sp., *Vitex negundo* L., *Areca catechu* L., *Areca* spp., *Ehretia microphylla* Lam, *Amaracarpus solomonensis* Merr. & Perry, *Buchanania solomonensis* Merr. & Perry, *Goniothalamus grandiflorus* Mark., *Barringtonia magnifica* Lauterb., *Syzygium nutans* K. Schum., *Aglaia nudibacca* C. de Candolle, *Evodia hortensis* Forst., *Psychotria Schmielei* Warb., *Cassia javanica* L., and *Licuala* sp.

Hibiscus tilliaceus and *Pandanus* are seldom found along the stream banks, appearing to be better adapted to the dryer outer edge facing the grassland. Both of these species are absent above the point where the streamside forests merge into the forests at the bases of mountain slopes.

The secondary forest layer trees are usually scattered, seldom forming pure stands except on those small streams that are dry too long to support larger trees. Here the secondary forest trees are the dominants, and in the case of *Erythrina variegata* L. often form continuous stands. This tree, usually at the outer edges of the streamside communities, flowers at the end of the rainy season producing a spectacular sight, for the forest wall for many miles becomes a solid bank of red flowers.

The breadfruit trees, *Artocarpus communis* J. and G. Forst., and *A. altilis* (Park.) Fosb. appear in all the streamside communities examined and always seem to be secondary. These species prefer the edges of the forest, being absent entirely from the shaded areas. *Cerbera manghas,* several species of *Barringtonia,* and the palms *(Pinanga, Areca)* all seek the actual stream banks, but may be at the outer edges occasionally, while *Mellia* sp. and *Erythrina variegata* are chiefly found fronting on the grass.

The strangling figs (*Ficus* spp.) reach large size often killing smaller trees and, though covering a large area with their roots, do not reach the heights of the primary forest trees. On other islands of the Solomons, such as Bougainville, this is not the case as the banyans reach enormous size and often stand many feet above the forest canopy.

Many tree species are represented in this stratum. Some of the more common are: *Hedycarya solomonensis* Hemsl., *Harpullia arborea* (Bl.) Radlk., *Colona scabra* (Sm.) Burret., *Canangium odoratum* (Lam) Baill., *Parinarium glaberrimum* Hassk., *Trema orientalis* Bl., *Litsea perglabra* Allen (This tree sometimes is very large), *Kleinhovia hospitata* L., *Dysoxylum caulostachyum* Mig., *Trichospermum psilocladum* Merr. & Perry, *Cordia cummingiana* Vidal., *Horsfieldia salomonensis* A. C. Smith, *Sterculia* sp., and *Antidesma* spp.

The primary forest layer is made up of trees usually 100 to 150 feet in height and constitutes the dominant vegetation of the lowland forests on all the larger Solomon Islands. On most of the large streams and on the meander flats this layer is continuous. On those parts of the north coast of Guadalcanal not within the influence of the rain shadow, that is, east of the Berande River, this forest type reaches its greatest development and from the air presents an almost unbroken canopy.

These trees are about equally divided among those with and without buttresses, and no apparent supremacy as to height was noted in either those with or without these supporting structures, although the buttressed trees as a whole tended to be more numerous.

This stratum is apparently the least tolerant of drought as shown by its distribution. In all cases it is absent along temporarily dry water courses and often is found only on the flood terraces cut by the streams. At a distance, the character of the bordering vegetation is a good index to the size and duration of a stream except in oxbow depressions and along very deep channels. In some of the smaller streams the large roots form a local base level by choking the stream and impeding channel deepening. Swamps are often caused in this way.

Some of the primary forest trees are: *Pterocarpus indicus* Willd., *Celtis Kajewski* Merr. and Perry, *Myristica platyphylla* A. C. Smith, *Intsia bijuga* (A. Gray) O. Ktze., *Canarium* spp., *Horsfieldia novoguineensis* Warb., *Alstonia longissima* (Muell.) Merr. & Perry, *Campnosperma Brassii* Merr. & Perry, *Pometia pinnata* Forst., *Elaeocarpus floridanus* Hemsl., *Rhus taitensis* Guill., *Spondias pinnata* (L.) Kurz., *Terminalia solomonensis* Exell., *Syzygium sumarangense* (Blume) Merr. & Perry, *Mangifera minor* Bl., *Inocarpus edulis* Forst., and *Calophyllum solomonense* A. C. Smith.

Lianes of the Primary Layer

Although most of the smaller climbing plants of this area are confined to the lower strata and the edges of the forests, larger ones reach the tops of the highest trees and form extensive masses in the crowns, often overtopping the supporting tree. This is especially true of the rattan palm (*Calamus Holrungii* Becc.) and some of the larger species of *Freycinetia.* The climbing aeroids such as species of *Raphidophora* also reach the upper levels, but are mostly confined to the boles where their large leaves form mosaics that obscure the trunks. *Mucuna gigantea* (Willd.) DC., *Derris trifoliata* Lour. and species of *Celastraceae* also reach the upper levels. The lianes are easily visible from the edges of the streamside forest and give a characteristic appearance of tangled cordage draped over the trees. The feathery leaves of the rattan palms give a deceptive softness to the outline of the clothed trees. In addition to the above, the following lianes are also found in the streamside communities: *Cissus assamica* (Laws.) Craib., *Cayratia trifolia* (L.) Domin., *Salacia prinoides* (Willd.) DC., *Parsonsia lata* Mgf., *Strychnos* sp., and *Allophylus leptococcus* Radlk.

Epiphytes of the Streamside

Epiphytes vary in number and kinds in the streamside communities and their distribution is dependent upon the periodicity of flow. Epiphytes are numerous on trees bordering large, permanent streams while along intermittent streams they are scarce and of different type, probably due to the much lower humidity along the latter water courses.

The total number of epiphytes on the streamside trees within the rain shadow is markedly less than on the same tree species in the forests of the lower mountain slopes, and even the lower mountain slopes of Guadalcanal within the rain shadow do not usually have as great or variable an epiphytic flora as do the lowlands of other Solomon Islands such as Bougainville.

The epiphytes of the streamsides are not much different from those of the strand, although the boles of streamside trees may be covered with mosses in the denser stands. It is interesting to note that the "ant plants" *Myrmecodia salomonensis* Becc. and *Hyd-*

nophytum Stewartii Fosb. were mostly confined to the trees along permanent streams, being very rarely seen on the smaller streams. The huge birds nest ferns *Asplenium macrophyllum* Sw. and *A. nidus* L. appear in considerable numbers along the large permanent streams and in the swamps at the bases of the mountains.

The Forest Edge

The striking feature of the streamside forest edge is its abrupt rise from the grassland (Fig. 10). At a distance the forest appears as a solid wall, and closer scrutiny confirms this impression. Interwoven with the plants of the shrub-small-tree layer are many species of climbing plants which form a mass of impassable vegetation. Cutting a path through the forest is difficult, unpleasant, and often dangerous for many plants are armed with thorns and spines; the rattan palm in particular has whip-like projections and recurved thorns that can inflict serious wounds.

The most colorful aspect of the vegetation appears along the forest edge. Early morning finds it literally ablaze with color. The scarlet bracts of the wild ginger, blues, reds, lavenders, and white of *Ipomoea*, deep purple of the climber (*Mucuna urens* DC.) with many others combine to make an entirely pleasing show.

Some of the climbers present in the forest edge are: *Cucumis sativa* L. (herbaceous), *Passiflora foetida* (DC.) Killip (A woody vine), *Ipomoea congesta* R. Br. (herbaceous, morning glory vine), *I. gracillis* R. Br. (herbaceous, morning glory vine), *Mucuna urens* L. (A large woody liana), *Benincasa hispida* (Thunb.) Cogn. (herbaceous), *Cassythe filiformis* L. (herbaceous), *Calamus* sp. (A large, climbing palm), *Lygodium* sp. (a climbing fern), *Freycinetia* sp. (a spiny leaved climbing member of the *Pandanaceae*), *Luffa cylindrica* (L.) M. Roem., *Araceae,* and many more.

These climbing plants form such close mosaic that only a few feet within the forest the shade is so intense that few ground layer plants can grow.

Deciduous Trees

Several of the trees of the streamside community lose their leaves during a portion of the dry season. Loss of leaves usually is most pronounced in late July to late November. At no time, however, are enough trees barren to give a naked appearance to the forest. Sufficient evergreen trees are intermixed to mask the effects of the deciduous types. Deciduous trees are not confined to the rain shadow area, and were observed in rain forests where no dry season occurs.

During the most severe portion of the dry season, the evergreen trees bordering the dry streams lose some of their leaves, and at this time the bottoms of the dry streams present an appearance not unlike those in temperate zones, for dry leaves accumulate giving a decided autumnal appearance. This condition was not seen anywhere other than in the rain shadow area.

It was noted that some trees such as *Erythrina variegata* L. lost all or most of their leaves before flowering at the end of the rainy season. Refoliation takes place immediately after flowering, however, and these trees are usually in leaf through part of the dry season.

Lowland Forest Association

The rain forest of the lower mountain slopes (to 800 feet) and the portion of the island not within the rain shadow is much more luxuriant than the streamside forests. The tree species found in the streamside forests are also found on the mountain slopes, but here a giant *Ficus*, a large *Canarium*, and *Calophyllum vitiense* Turill. dominate the forest. *Calophyllum vitiense* is the characteristic tree of this forest. This tree grows to over 120 feet in height on many of the slopes and ridges of the river canyons.

Smaller trees are abundant, and many that do not appear in the streamside forests and low forests below 400 feet are encountered. Among these are: *Aglaia Goebeliana* Warb., *Pittosporum ferrugineum* F. Vill., and *Cyathocalyx petiolatus* Diels.

MID-MOUNTAIN FOREST BELT

Higher on the mountain slopes (800 to 1,500 feet) the rain forest dominants as listed before still predominate, but the number of smaller trees increases markedly. These trees are also different from those of the lower altitudes, although some of them have a lower altitudinal range in the bottoms of river canyons. Some of these smaller trees are: *Litsea solomonensis* Allen, *Commersonia bartramia* (L.) Merr., *Garcinia salomonensis* A. C. Smith, *Colona velutina* Merr. & Perry, *Canthium Karrense* (Val.) Kaneh., *Gnetum gnemone* L. (Common at sea level on other Solomon Islands), *Ficus* spp., *Psychotria* sp., and *Breynia cernua* Muell.

On the banks of creeks *Saurauia conferta* Warb. is common, and *Medinilla cephalantha* Merr. & Perry is abundant in the humid gullies on the mountain sides.

The parasitic tree *Fagraea solomonensis* G. & B. which often reaches 12 to 18 inches in diameter appears on the trees of mountain slopes only. This plant is found on several hosts.

Many vines tangle in the rain forest trees. These include most of the lianes of the lowland forests and especially *Freycinettia* which is very abundant on the trees of the river canyons. In addition to the common lianes of the lowlands, *Carruthersia Brassii* Merr. & Perry, *Uncaria philippinensis* Elmer, and *Hippocratea* sp. climb on the rain forest trees.

UPLAND FOREST BELT

The higher mountain slopes above 3,000 feet are covered with a high forest dominated by giant trees which are over 100 feet in height. These tend to become scattered as the slope increases in height and steepness, and are absent entirely from the ridges. The ridges are covered with low shrubs, gnarled small trees and vines. Epiphytes of all types are abundant.

The larger trees of the upland forests are: ***Myristica solomonensis*** Warb., ***Myristica Kajewski*** A. C. Smith, *Sterculia* sp., ***Polyosma macrobotrys*** Mattf., *Ficus* sp., *Sloanea insularis* A. C. Smith, and *Eleocarpus fauroensis* Hemsl.

There are many medium sized trees in the uplands. One, a conifer, (*Dacridium xanthandrum* Pilg.) is very rare being found only on soils heavily impregnated with copper and gold ores. Some of the more common are: *Astronidium muscosum* Merr. & Perry, *Pygeum Schlechteri* Koehne, *Astronidium montanum* Merr. & Perry, *Ficus* sp., *Alphitonia* sp., *Perrottetia molucana* (Bl.) Loes., *Mastixia philippinensis* Wang., *Tridiaspernicum Kajewski* Merr. & Perry, and *Evodia Radlkoferiana* Ltb.

The abundance of small trees is quite characteristic of this forest especially on the steeper slopes and ridges. On the very rough rocky ridges *Parasponia paucinervia* Merr. & Perry is the characteristic tree and is seldom more than 25 feet high. Other common small trees are: *Coulthovia novo-britannica* Kaneh. & Hat., *Saurania Schumanniana* Diels., *Carpodetus amplus* Reed, *Litsea papillosa* Allen, *Belliolum Kajewski* A. C. Smith, *Dolicholobium callianthrum* Merr. & Perry, *Harpullia vaga* Merr. & Perry, *Leea macropus* Ltb. & K. Sch., *Leea indica* (Burm.) Merr., *Semicarpus decipiens* Merr. & Perry, and *Ficus* sp.

The undercover is rich in shrubs which clothe the slopes and ridges and make a very dense tangle under the trees. Among these shrubs the following are representative: *Rubus Brassii* Merr. & Perry, *Ceodes umbellifera* J. R. & G. Forst., *Dolicholobium Kajewski* Merr. & Perry, *Ophiorrhiza solomonensis* Merr. & Perry, *Lasianthus chlorocarpus* K. Sch., *Bochmeria* sp., *Medinilla rubescens* Merr. & Perry, and *Melastoma polyanthum* Bl.

Lianes are very numerous and often climb to the tops of the trees. There are more different kinds of lianes at this altitude than at any other elevation on the island. Some of these lianes are: *Strongylodon lucidus* Seem., *Psychotria olivaceae* Val., *Tetrostigma pergamaceum* Planch., *Cissus simplex* Bl., *Cayratia japonica* (Thurb.) Gagnep., *Tetrostigma aff. maluense*, *Rubus moluccanus* L., *Chitandropsis novoguineensis* Wernh., *Jasminum didymum* Forst., and *Medinilla calliantha* var. *bella* Merr. & Perry.

The tops of the mountains above 4,000 feet are covered with low gnarled shrubs and trees, but no collections have been made above 4,200 feet, so the higher mountains of Guadalcanal are entirely unknown floristically. At least two mountains on this island are over 7,000 feet and Mount Popomanasiu reaches 8,005 feet. These mountains should be of great interest to both taxonomists and ecologists.

The plants dominating the tops of mountains at 4,000 to 4,200 feet are all low shrubby plants or low gnarled trees. The known trees and shrubs are: *Belliolum gracile* A. C. Smith, *Pittosporum* sp., *Symplocos* sp., *Cyphalophus* sp., *Astronidium anomalum* Merr. & Perry, *Gnetum* sp., *Claoxylon* sp., *Decaspermum coriandri* (Bl.) Diels, and *Tristania* sp.

GRASSLAND FORMATION

The grasslands of Guadalcanal are the only large grass areas in the Solomon Islands. Small grass areas are found in the Florida Islands which are probably due to the rain shadow cast by the lofty mountains of Guadalcanal, and some grassland is found on Buka, a low island north of Bougainville (Navdocks—101, p. 19). This island is so situated that this grassland may be due to a rain shadow cast by the high mountains of Bougainville.

The grassland of Guadalcanal and Florida Islands is an almost pure stand of *Themeda triandra* Forsk; that on Buka was not seen by the writer. On Guadalcanal *Phragmites Karka* (Retz.) Trin. is dominant locally in low places where water stands after rains. This tall reed is a good indicator of standing water in the grasslands and was so used to locate areas needing attention for malaria control. Small areas near palm groves were covered by the snowy plumed *Imperata cylindrica* (L.) Beauv. but this grass is probably an introduced species and is not able wholly to occupy the dry areas covered by *Themeda triandra*.

FIG. 12. The dominant grass of Guadalcanal grows from four to six feet high. The high, plumed plant above the grass is a species of *Phragmites* which reaches ten feet in height. The African Oil Palm *(Elaeis guineensis)* can be seen in the right background.

The dominant grass *(Themeda triandra)* is from 4 to 6 feet in height, is a good fodder for cattle, and was used for that purpose before the war. It forms tussocks as a result of erosion. The dead culms become interwoven making travel through the grass difficult.

During the dry season the grass is yellow-brown in color, and usually dead and dry. Little growth takes place during the dry season, and if burning occurs new green shoots appear only after a rain. After the rainy season begins, the grass takes on a greener appearance which is still tinged with the brown of the dead remnants of the dry period. In the few months of the rainy season this grass, as observed on burned areas, grows to a height of 5 feet. Florets appear in February and by the end of March seeds are well formed in loose panicles. The geographic distribution of *Themeda triandra* extends

from Africa to China, Australia (Hitchcock, 1936) and the Solomon Islands.

The tall reed *(Phragmites Karka)* blooms in March and adds scattered patches of plumes to the general aspect. During the dry season it loses all its leaves and only the dry culms stand. This plant sends out long rhizomes on the surface of the soil. The natives make arrows of the culms.

On the north coast of Guadalcanal the major portion of the area from the Berande River west to, and including, Mt. Esperance is covered by grass. These steppes reach their greatest depth on the coastal plain between the Balesuna and Lunga Rivers, but they also extend inland several miles on the ridges to the west of the Lunga River. From the sea the northwestern portion of Guadalcanal has a park-like appearance.

On the low mountains of the western end of the island and the upper limits of the grasslands, a near savannah type of vegetation occurs. Isolated patches of shrubs and small trees cling to the small ravines where moisture collects. Slope control is a major factor here, and apparently these hills receive just enough additional water from their height to account for this scattered intermediate vegetation. This area indicates a transitional stage between the grassland and the forest type and is considered to be additional evidence of a water controlled vegetation, that is, evidence of a rain shadow.

There are several places on the mountains above Henderson Field that appear to have been old fields where native gardens had been cleared in the past. In such a ecotonal area the clearing of the forest would give the grass an opportunity to extend its control. Study of this area revealed that most of the straight lines are associated with changes in slope, but it is still probable that some of these grass areas are due to man's interference in an unstable area.

SUCCESSIONAL CHANGES

During establishment of military camps on Guadalcanal large areas of grasslands were destroyed. After these camps were abandoned many areas grew back to the native grasses, and during the course of the war, camps were being established and abandoned regularly in many different places so that practically all stages of succession from bare ground to ultimate restoration of the native grasses were available for study.

Succession took two courses depending on what time of the year the bare areas were abandoned. If this took place during the dry season the ground often remained quite barren for a considerable time and the pioneers were usually herbs such as *Portulaca oleracea* L., *Euphorbia hypericifolia* L., *Amaranthus viridus* L., *Stachytarpheta jamaicensis* (L.) Vahl., and others. These herbs were soon followed by small shrubs *Sida rhombifolia* L., *S. spiraeifolia* Willd. and *Mimosa pudica* L. During the wet season succession proceeded in a more luxuriant manner. Within a month the barren area would be covered by mixed herbs and shrubby plants including those mentioned above, and in addition the following: *Physallis angulata* L., *Carica papaya* L., *Phragmites Karka, Macaranga tanarius* (L.) Muell., *Cyperus umbellatus* Naves, *Vernonia cinerea* (L.) Less., *Ageratum conyzoides* L., *Alternanthera sessilis* R. Br., and *Borreria laevis* (Lam) Griseb. Besides these plants many species, forming a weedy layer under the palm groves, occur in these pioneer situations.

In every case where grass was destroyed the native grass *(Themeda triandra)* ultimately reinvaded the destroyed areas. Often this grass would take over without the previous pioneer stages mentioned above. The grass succeeds in these areas during the dry season when most of the herbaceous plants die for lack of water, and is capable of overtopping the small shrubs. It was noted that holes made by exploding bombs, trenches, and other depressions held sufficient water to allow certain plants to persist for some time in the dry season, but only very large depressions were capable of holding enough water to allow invading species to live through the entire dry season.

In those few places where streamside forests were destroyed, a weedy pioneer stage was noted, but this was soon crowded out by shrubs and young forest trees or by bamboo. *Themeda* apparently is unable to invade any of the streamside situations even after the forest is destroyed.

NUT PLANTATIONS

Many large plantings of coconut palms *(Cocos nucifera)* have been made all along the north coast of Guadalcanal including the grassland. One small grove of the African oil palm (*Elaeis guineensis* Jacq.) was observed which did not appear to be very successful. These palms were planted in the grasslands. Trees were constantly dying, apparently from a fungus that attacks the boles at the soil line, causing decay and eventually undermining the tree until it falls. Only small amounts of nuts were produced, most of the trees apparently being sterile. This palm has escaped from cultivation and forms dense groves on the banks of the Little Tenaru River downstream from the planted area. None of the escaped palms was bearing fruit. The rough boles of this palm provide optimum conditions for the establishment of epiphytes and the healthy trees have a large crown that gives a great amount of shade.

Among the epiphytes seen on these trees are: *Ficus* sp. (The strangling fig), *Polypodium* sp., *Nephrolepis biserrata* Schott., *Nephrolepis hirsutula* Presl., *Vittaria lineata* Sw., *Asplenium nidus* L., and *Davallia solida* (Forst.) Sw. Mosses and several unidentified large orchids are also found here. During the dry season most of the epiphytes on these trees dry up and die, but during the wet season the boles are entirely obscured by ferns and mosses.

During the war these palm groves were neglected and became heavily infested with weeds. Many of these weeds may have been introduced during military operations.

Seedlings of *Cocos nucifera* L. were so dense in neglected palm groves that passage was difficult. This

condition was most noticeable in groves near streams or low areas where water was available throughout the year. Germinating coconuts were observed to die in the grassland areas where a dense shade was not present to offset the conditions of the dry season. Perhaps irrigation of young plantings until the roots can reach the water table would make it possible for the entire grassland on the plains to be successfully operated as plantations.

Themeda triandra grows to full size in the edges of coconut groves, and was observed to be very successful in the groves that have been planted in grassland areas. The following grasses thrive in the groves: *Echinocloa colonum* (L.) Link., *Digitaria microbachne* (Presl.) Heur., *Panicum reptans* L., *Eragrostis amabilis* (L.) Hook and Arn., *Eleusine indica* (L.) Gaertn., *Centotheca latifolia* (Osb.) Trin., *Pennisetum macrostachyum* (Brogn.) Trin. (forms dense mats in moist groves), and *Coix lachryma-jobi* L.

Many herbaceous weeds add to the diversity of the plant cover beneath the palms. These weeds seem to have no definite niche as to positions in the grove, simply inhabiting any space available where competition is not too great. Some of them are: *Emilia sonchifolia* (L.) DC., *Ageratum conyzoides* L., *Stachytarpheta jamaicensis*, *Asclepias curassavica* L., *Euphorbia hypericifolia* L., *Alternanthera sessilis* R. Br., *Jussieua suffructicosa* L., *Amaranthus viridis* L., *Arachis hypogaea* L., *Pouzoulzia zeylandica* (L.) Benn., *Eclipta alba* (L.) Hassk., *Siegesbeckia orientalis* L., *Physallis angulata* L., *Hibiscus abelmoschus* L., *Hemigraphis colorata* (Bl.) Hallier, *Pseuderanthemum* sp., *Helminthostachys zeylanica* (L.) Hook, *Erechtites valerianifolia* DC., and *Uraria lagopodioides* DC.

Plants other than grasses that form mats are represented by *Commelina nudiflora* L. and *Desmodium triflorum* (L.) DC. The tiny blue flowers of *Commelina nudiflora* L. add color to the most shaded areas while the low, clover-like *Desmodium* prefers more open areas where it forms extensive, dense, lawn-like mats.

Many colorful plants bloom in the groves such as *Geodorum nuttans* (Presl.) Ames. a pink ground orchid, *Curculigo orchoides* Gaertn. a yellow flowered member of the *Amaryllidaceae* which blooms at the soil line; *Canna indica* L. a small, scarlet flowered plant; *Costus speciosus* Bl., *Globba* sp., and *Capsicum frutescens* L. which is very colorful as the small peppers ripen.

In wet areas many weedy plants are found which seem unable to compete in less favored positions. Among these are: *Borreria laevis* (Lam) Griseb., *Nephrolepis biserrata* Schott., *Dryopteris* sp., *Cyperus* sp., *Fimbristylis diphylla* Vahl., *Kyllingia brevifolia* Rottb., *Bonnaya veronicaefolia* (Betz.) Spreng., *Hedyotis* sp., *Vernonia cinerea* L., and mosses.

Shrubby plants make up the dominant portion of the weed cover in the palm groves and many young forest trees were seen in this group which include: *Macaranga tanarius* (L.) Muell., *Sida rhombifolia* L., *Mimosa pudica* L., *Cassia alata* L., *Abutilon indicum* (L.) Saucet., *Melochia indica* A. Gr., *Leucena forsteri* Benth., and *Maesa* sp.

Many climbing and trailing plants are also found in this situation: *Ipomoea batatas* Poir., *I. gracillis* R. Br., *Momordica charantia* L., *Aniseia martinicensis* (Jacq.) Choisy, *Merremia linifolia* Bl., *Cucumis sativa* L., *Lygodium circinatum* (Burm.) Sw., *Passiflora foetida* (DC.) Killip, and *Mucuna urens* DC.

DISCUSSION

There is evidence from the writings of Brass (1938) and Lam (1934) that it is not safe to assume that all grasslands of the tropics are the result of burning by man. The natives of New Guinea practice burning grass as an aid to hunting wild pigs. It has been assumed by some writers that the grass has been extended by the burning at edges of the forests. The natives of the Solomon Islands have a superficially homogeneous culture which apparently does not include burning of grass to hunt pigs. In all the time spent in those islands only two cases of burning of grass were noted and both of these were started by white men. The pigs on Guadalcanal were only seldom found in the grass, and it is difficult to see what advantage could be gained by burning grass to hunt since the grass is high right to the edge of the forest, and the pigs would only have to run into the tangled streamside forest to lose themselves.

The native population of the Solomon Islands is scattered throughout the islands primarily in forested areas. There is ample evidence that they have been distributed in this manner for centuries. There is, however, no grassland anywhere in the Solomon Islands other than where local topographic conditions reduce the rainfall. Obviously their activities could not be responsible for the grasslands.

CONCLUSIONS

1. The plant formations of the north coast of Guadalcanal are modified by lowered and disproportional seasonal distribution of the rainfall.

2. This difference in plant formations is due to the rain shadow.

3. The grassland is not a product of fire and is remaining relatively static as to its relations with the forest.

SUMMARY

1. The writer was in the Solomon Islands for 22 months, during which time he spent a year on Guadalcanal and the remainder on a ship which touched at many other Solomon Islands.

2. Guadalcanal is one of the southern islands of the Solomon group and is characterized by having a rain forest on the south side and grasslands on the north side. It is the only island of the group having a mountain chain at right angles to the prevailing wind direction.

3. The ecological factors responsible for the grass-

lands of Guadalcanal are both climatic and topographic. The adiabatic effect of rising winds approaching the island from the southeast causes a rain shadow to be cast on the northwest side of the island. In the rain shadow insufficient rain falls during several months to support a forest. The grassland is not due to fires or soil deficiencies.

4. The general aspect, floristics, strata, and limiting ecological factors of the vegetation units were used to classify the vegetation into three formations, four belts, and seven associations.

5. The successional changes in destroyed grassland always terminate in a grass climax. The succession where forest was destroyed was in the direction of reforestation.

6. It is not safe to assume that all grasslands of the tropics are the result of fire or human destruction.

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